

SYSTEMATICS OF THE SCUTELLARIA ANGUSTIFOLIA COMPLEX (LABIATAE)

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INTRODUCTION

The *Scutellaria angustifolia* complex (Labiatae) comprises nine species of herbaceous perennials native to western North America. These taxa form a morphologically cohesive group characterized by thickened underground rhizomes, relatively large flowers (12–35 mm long) borne individually in the upper leaf axils, and black, circumferentially banded nutlets. The center of diversity of the *S. angustifolia* complex is in northern California and adjacent portions of Oregon and Nevada, where the group has undergone a phylogenetic radiation into a wide variety of habitats, including streamsides, conifer and oak woodlands, chaparral, and sagebrush deserts.

Scutellaria L. is a genus of approximately 200 species (Cronquist 1981a), with a world-wide distribution. The genus was included by Linnaeus in *Species plantarum* (1753), but the name initially was proposed by Rivinius (Linnaeus 1735). The derivation of the name has been attributed variously to the Latin words *scutella*, dish or small tray, or *scutellum*, shield. In either case, this refers to the transverse crest typically found on the upper lobe of the calyx. The common name, skullcap, refers to the same distinctive feature.

Scutellaria is readily distinguished from other members of the mint family (except *Salazaria* Torr.) by the two-lobed calyx with its distinctive crest and the androecium consisting of two pairs of stamens with one aborted anther sac in each anther of the lower staminal pair. *Salazaria*, a monotypic genus of the American Southwest, shares these distinctive characters with *Scutellaria*, but is distinguished from it by the swelling of the calyx at maturity, thereby prompting Epling (1942) to refer to *Salazaria* as: “a *Scutellaria* with inflated calyx.” Primarily based on pollen morphology, *Scutellaria* is placed in the ancestral subfamily Lamioideae, in the two subfamily system of Erdtman (Erdtman 1945; Cantino & Sanders 1986). However, Briquet (1895) placed *Scutellaria* and *Salazaria* in a distinct subfamily, Scutellarioideae, based on the distinctive features mentioned above.

Three sections were recognized in the first monograph of *Scutellaria* (Hamilton 1832): *Lupulinaria*, *Stachymacris*, and *Galericularia*; the last contained *S. angustifolia*, the only species of the *S. angustifolia* complex described by that time. Subsequently, Bentham (1832, 1836, 1848) expanded Hamilton’s sectional classification to five sections, adding two new species of the *S. angustifolia* complex, *S. antirrhinoides* and *S. tuberosa*, to section *Galericularia*. When Briquet treated the mint family for *Die natürlichen Pflanzenfamilien* (Briquet 1895), all species currently recognized in the *S. angustifolia* complex, except *S. sapphirina*, were described.

Penland (1924) was the first to undertake a treatment of the North American species of *Scutellaria*. Penland’s treatment relied heavily on morphology of the nutlets and included a key to species based entirely on nutlet characters. Leonard

(1927), utilizing a greater number of characters, produced a more complete monograph of the North American species of *Scutellaria*. The most recent monograph was published by Epling (1942) and is the most comprehensive treatment of all New World species to date. Epling added many new names and combinations to the nomenclature of *Scutellaria*, including a revised sectional classification for the New World taxa. The large section *Galericularia* was treated by Epling as several smaller sections. In section *Galericularia*, he retained two South American species, *S. racemosa* and *S. platensis*, four taxa comprising the *S. parvula* complex in eastern North America, the circumboreal *S. galericulata*, and all of the taxa of the *S. angustifolia* complex distributed in western North America. Since Epling's treatment, most work on *Scutellaria* in North America has been floristic, notably Cronquist's treatment of the genus for the *Intermountain Flora* (Cronquist 1981b; Cronquist et al. 1984) and Lane's treatment for the *Flora of the Great Plains* (Lane 1978, 1987). A monograph of Epling's section *Annulatae* was prepared by Collins (1976).

The taxonomic treatment presented here represents an integration of character variation and phylogeny in the *Scutellaria angustifolia* complex. The results recognize that the *S. angustifolia* complex may not be strictly monophyletic and that additional information may require subsequent realignments.

Questions remain for future analyses regarding the phylogenetic disposition of particular taxa within the *S. angustifolia* complex, as circumscribed in this study, and of taxa related to the group. Does *S. tuberosa* belong to a monophyletic group with the rest of the *S. angustifolia* complex, or does it have a closer phylogenetic relationship elsewhere in *Scutellaria*? Are *S. nervosa* and *S. parvula* part of a monophyletic group with the *S. angustifolia* complex? Where does *S. stachyoides* fit into a phylogenetic scheme for *Scutellaria*? The last species, placed with the *S. angustifolia* complex by Epling (1942) in his section *Galericularia*, is known only from the type locality in southern Sonora and seems better placed in section *Resinosae* (close to *S. microphylla* and *S. drummondii*), based on characters of habit, pubescence, leaf shape, and distribution. Nutlets provide the most distinctive characters to differentiate the two sections and, unfortunately, the sole collection of *S. stachyoides* contains no mature fruit.

An isozyme analysis of 106 populations representing all nine species in the *S. angustifolia* complex and two outgroup species was conducted in connection with the systematic revision of the group to aid in the circumscription of taxa and to be used in conjunction with the morphological analyses to infer phylogenetic relationships (Olmstead 1989). Estimates of population genetic diversity within and among populations of each species were calculated to provide insight into the population structure and differentiation among species within the complex (Olmstead, in press).

In this treatment, an effort is made to delimit species and subspecies that are evolutionarily cohesive. Preferably, each is monophyletic, but some taxa may represent paraphyletic groups of populations. To do so, data from isozyme analysis are used to estimate the genetic relatedness among representative populations of all the species in the group. This assessment provides a basis for defining taxa and recognizing genetic discontinuities between taxa that is independent of morphology. Many morphological variants, previously recognized taxonomically, are shown by this study to represent variation among populations within genetically homogeneous species. Subspecies are recognized only for major morphological variations within a species that are geographically distinct or have distinct habitat preferences. Little is

known regarding the actual or potential interbreeding among species within the group, although a case of natural hybridization between *S. californica* and *S. antirrhinoides* has been documented (Olmstead, unpubl.).

MORPHOLOGY

Habit. All members of the *S. angustifolia* complex are herbaceous perennials capable of reproducing vegetatively by rhizomes. The individual plants (stems, roots, and proximal portions of the rhizomes) die at the end of the growing season, usually triggered by the onset of summer drought. The exception is *S. californica*, in which root crowns may occasionally produce shoots in successive years while also producing rhizomes. The most common growth form is a single or few-branched erect stem, typical of *S. angustifolia*, *S. antirrhinoides*, *S. brittonii*, *S. californica*, and *S. siphocampyloides*. *Scutellaria bolanderi* is usually found in shaded stream margins. It obtains its maximum height (70–80 cm) only when supported by surrounding vegetation; otherwise it may exhibit a decumbent main stem with erect lateral branches. *Scutellaria nana* and *S. sapphirina* have a dwarf, tufted habit resulting from branching at the lower nodes and very little internode elongation. This habit seems invariant in *S. nana* in field and greenhouse situations; however, in shady or moist environments, *S. sapphirina* will develop an erect, few-branched habit typical of other species in the group. *Scutellaria tuberosa* exhibits a stunted, usually unbranched, habit, producing only one or two flowering nodes when growing under mature chaparral, but following a fire *S. tuberosa* exhibits an erect, multibranched habit.

Rhizomes. The rhizomes of the *S. angustifolia* complex are typically smooth, yellow, and moniliform proximal to the stem, swollen with constrictions at the nodes distally, and extending 3 to 15 inches from the “mother” stem. The rhizomes of *S. tuberosa* differ from others in the group in having the moniliform portion end abruptly in a short, white, rugose tuber. The tubers of *S. tuberosa* undergo a period of dormancy for several months during which time neither cold treatment nor water nor a combination of the two can induce sprouting (personal observation). The rhizomes typical of the rest of the *S. angustifolia* complex, when severed from their “mother” stem, will sprout immediately given suitable conditions.

Indument. Three types of trichomes are found on the stems, leaves, and flowers of this group. Type I: Short (0.1–0.2 mm), unicellular trichomes are characteristically appressed or curved either upwards or downwards along the growth axis. The direction of curvature is usually characteristic for a species; ascendent in *S. angustifolia*, *S. antirrhinoides*, *S. californica*, *S. siphocampyloides* and descendent in *S. brittonii*, *S. nana*, and *S. sapphirina*. The most variable taxon for this character is *S. siphocampyloides*, in which a form without hairs, or only with minute scabriles, exists in a portion of the North Coast Ranges of California and a form with appressed descending trichomes exists in the inner South Coast Ranges of California (Figs. 1a, b). Type II: Long (1.0–3.0 mm), spreading multicellular trichomes are found in *S. bolanderi* (where they are occasionally gland-tipped) and *S. tuberosa* (Fig. 1c). The two taxa characterized by this type of trichome lack the shorter type I trichomes. Type III: Gland-tipped trichomes (0.5–1.0 mm long) occur in all taxa of the group, except for *S. sapphirina* and *S. tuberosa* (Fig. 1d). In no species are type III trichomes observed to exist in all populations. Populations are fixed generally for the presence or absence of type III trichomes, but several collections from two

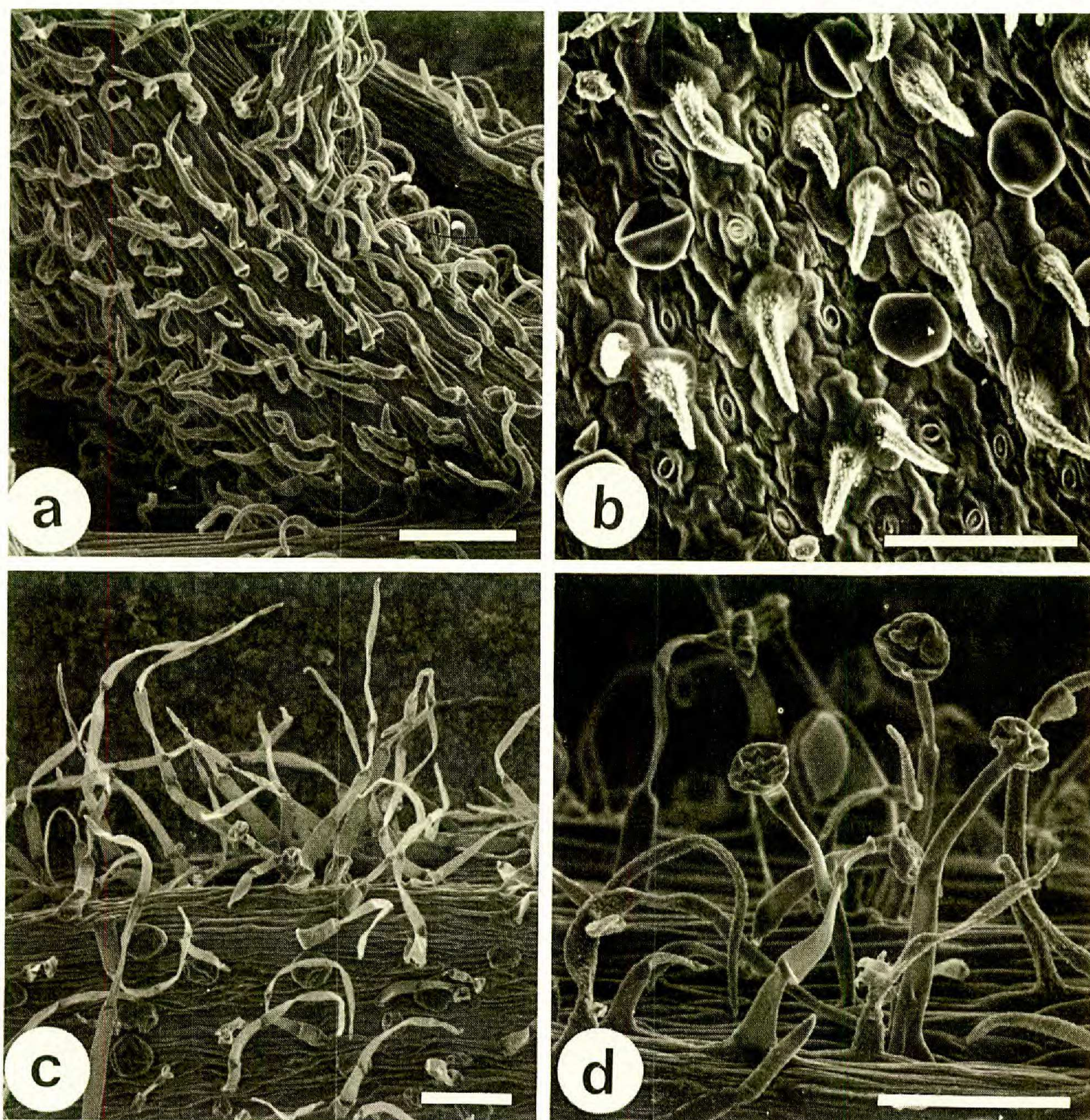


FIG. 1. Scanning electron micrographs of stem and leaf trichomes of *Scutellaria*. a. Type I trichomes, appressed and ascending on stem of *S. siphocampyloides* (Olmstead 813). b. Type I trichomes and sessile glands on leaf surface of *S. angustifolia* subsp. *angustifolia* (Olmstead 500). c. Type II trichomes and sessile glands on stem of *S. bolanderi* subsp. *austromontana* (Wiggins 2694). d. Type III (gland-tipped) trichomes with curved type I trichomes on stem of *S. siphocampyloides* (Olmstead 568). Scale bar = 0.1 mm.

species, *S. nana* and *S. siphocampyloides*, indicate that type III trichomes can be polymorphic within a population. The distribution of populations bearing gland-tipped trichomes usually is restricted to a portion of the range of a species, but may occur in scattered locales throughout the range of a species.

A reliance on type of indumentum in defining taxa in past treatments in *Scutellaria* has led to a proliferation of taxa unsupported by other substantial characters. In particular, the distribution of gland-tipped (type III) trichomes vs. short (type I) trichomes has been used as a species-defining character without recognizing that the type I trichomes co-occur with the more prominent type III trichomes and that the two types of trichomes represent distinct characters. Further discussion of indument as it relates to the systematics of the group is found in the appropriate species discussions.

Leaves. Leaves of members of the *S. angustifolia* complex vary in size, shape, margin, and texture. Considerable variation often exists within a single plant between leaves low and high on a stem. Basal leaves tend to be petiolate, often with the petiole equal in length to the blade, and may have crenate margins, whereas leaves in the upper, flowering portion of the same stem are sessile and have entire margins (except as noted below). For uniformity when comparing leaf size and shape of different plants, standardization was obtained for developmental differences by always measuring leaves at the first flowering node on a stem. In two species, *S. bolanderi* and *S. tuberosa*, all leaves have crenate margins, whereas in three species *S. antirrhinoides*, *S. californica*, and *S. siphocampyloides*, the lowermost leaves may be crenate, but the upper leaves (beginning at or below the first flowering node) are entire. In four species, *S. angustifolia*, *S. brittonii*, *S. nana*, and *S. sapphirina*, all leaves have entire margins.

The typical leaf shape is ovate to oblong, but in *S. bolanderi* the leaves are cordate, and in *S. nana* and *S. sapphirina* they tend to be rhomboid to obovate. Substantial variation in leaf size exists in all species in the group, but the ratio of leaf length to leaf width is a more conservative indicator of subtle shape differences among species with otherwise similar vegetative morphology. Mean length/width, with standard deviations in parentheses, for five taxa that are otherwise nearly indistinguishable vegetatively are as follows: *S. angustifolia* subsp. *micrantha*, 2.4 (0.3); *S. antirrhinoides*, 2.9 (0.5); *S. californica*, 2.9 (0.5); *S. angustifolia* subsp. *angustifolia*, 3.9 (0.8); *S. siphocampyloides*, 5.7 (1.5). The leaves of *S. brittonii* are distinct in that the midrib and primary lateral veins stand out prominently on the abaxial surface.

Inflorescence. Plants of the *S. angustifolia* complex bear individual axillary flowers. After the onset of flowering, flowers are produced continually as the stem grows indeterminately until favorable growing conditions cease. Differences exist among taxa in the amount of vegetative growth prior to flowering, from as early as 3–6 nodes above the base of the stem for *S. angustifolia* subsp. *micrantha* to as late as 10–15 nodes above the base of the stem in *S. bolanderi*.

Calyx. *Scutellaria* is defined primarily by two unique characters of the calyx. It consists of two lobes, instead of five, as is typical for mints, and it bears a transverse crest, or “scutellum”, on the upper lobe. The calyx is persistent after anthesis, closing at its mouth after the corolla is shed, thus enclosing the developing nutlets. The upper lobe of the calyx is deciduous at maturity, allowing release of the nutlets. A considerable degree of variation in calyx morphology exists within the genus, particularly in size and orientation of the scutellum. In the *S. angustifolia* complex, the scutellum is typically as broad as the calyx, erect, and strongly concave posteriorly. The calyces of most species in the group are indistinguishable from one another; only two species are distinct. The scutellum in *S. bolanderi* is slightly scalloped giving the crest a somewhat crenate outline. The scutellum in *S. tuberosa* is not as broad as in other members of the group and is shallowly concave to subconical.

Corolla. The corollas of plants in the *S. angustifolia* complex are recurved-ascendent near the base, bilabiate, 12–35 mm long, and personate (closed at the throat by an arch projecting upward from the lower side of the corolla tube). The upper lobe of the corolla forms a galea enclosing the anthers and stigma. Corolla color in the *S. angustifolia* complex is either violet-blue, usually with a white patch on the lower lip, or white. The lower lip is frequently mottled with violet-blue or purple spots in flowers of either color (the mottling occurring in the white patch of blue-violet flowers), but may be of uniform color, either violet-blue or white, or may bear

an unmarked white patch. All combinations of lower lip markings (with or without a white patch and with or without mottlings) can occur in two of the blue-flowered species, *S. angustifolia* and *S. siphocampyloides*, which suggests that such markings are of little taxonomic importance among the blue-flowered species in the group. The variation in color markings among the three white-flowered species is more distinctive than among the blue-flowered species. *Scutellaria californica* has no markings on the lower lip, and the corolla is usually uniformly white but may be tinged with pale blue or pink. The corollas of *S. bolanderi* are white-mottled with blue on the lower lip. The corollas of *S. nana* are creamy-yellow to ochroleucous, usually mottled with purple on the lower lip, and frequently tinged with purple on the dorsal surface.

Corolla length is extremely variable within taxa of the *S. angustifolia* complex. However, mean corolla lengths of species fall into two distinct groups. Three taxa, *S. angustifolia* subsp. *angustifolia*, *S. brittonii*, and *S. siphocampyloides*, have mean corolla lengths of 25–27 mm, whereas the remaining taxa all have mean corolla lengths of 15–17 mm. A survey of taxa outside the *S. angustifolia* complex for outgroup comparison suggests that the smaller, 15–17 mm, corolla size is ancestral within the group and the large flower sizes are derived (Olmstead 1989).

Androecium. The androecium of *Scutellaria* consists of two pairs of stamens, the lower pair (adnate to the lower side of the corolla tube) is slightly longer than the upper pair (adnate to the upper side of the corolla tube) and arches above them in the galea formed by the upper lobe of the corolla. Each stamen of the lower pair has one fertile and one aborted anther sac; the upper pair has both anther sacs fertile. The stamens of the *S. angustifolia* complex are typical for the genus and do not differ from one another in any consistent fashion. The free portion of the filaments are pilose, and the anthers are ciliate along the suture. Sessile glands containing a milky substance are attached to the anthers near the point of attachment to the filament.

Gynoecium. The gynoecium is composed of four basally attached mericarps located on top of a swollen gynoecial disk. The disk is greenish yellow in all species except in *S. nana*, in which it is orange-red. Orange-red gynoecial disks also are found in *S. nervosa* and *S. parvula* of eastern North America; both are closely related to the *S. angustifolia* complex, but it is uncertain whether similarity in color of gynoecial disks is indicative of close phylogenetic relationship between these two taxa and *S. nana*.

Nutlets. The mature mericarps of *Scutellaria*, referred to as nutlets, were examined by Penland (1924) in a study of North American species and by Lane (1983) in a study of the Great Plains species. Both studies note the value of nutlet morphology in defining species groups in *Scutellaria*. Using the scanning electron microscope, Lane (1983) identified several potentially important systematic characters involving the size of nutlets, shape and size of surface papillae, presence or absence of a circumferential band without distinct papillae, presence or absence of sessile glands, and the shape of epidermal cells. He surveyed a group of species representing several major species groups, but with few closely related species among them, so the value of scanning electron microscopy of nutlets to species level systematics in *Scutellaria* cannot be determined from his study.

Nutlets for studies of nutlet morphology by scanning electron microscopy were obtained in the field, from greenhouse-grown plants, or from herbarium sheets. The nutlets were mounted on stubs using silver paste, coated with gold-palladium, and examined with a Jeol JSM U-3 scanning electron microscope. Nutlets of the *S. angustifolia* complex vary in color, size, shape and size of papillae, the presence or absence of a circumferential band, and the shape of epidermal cells (Figs. 2–4).

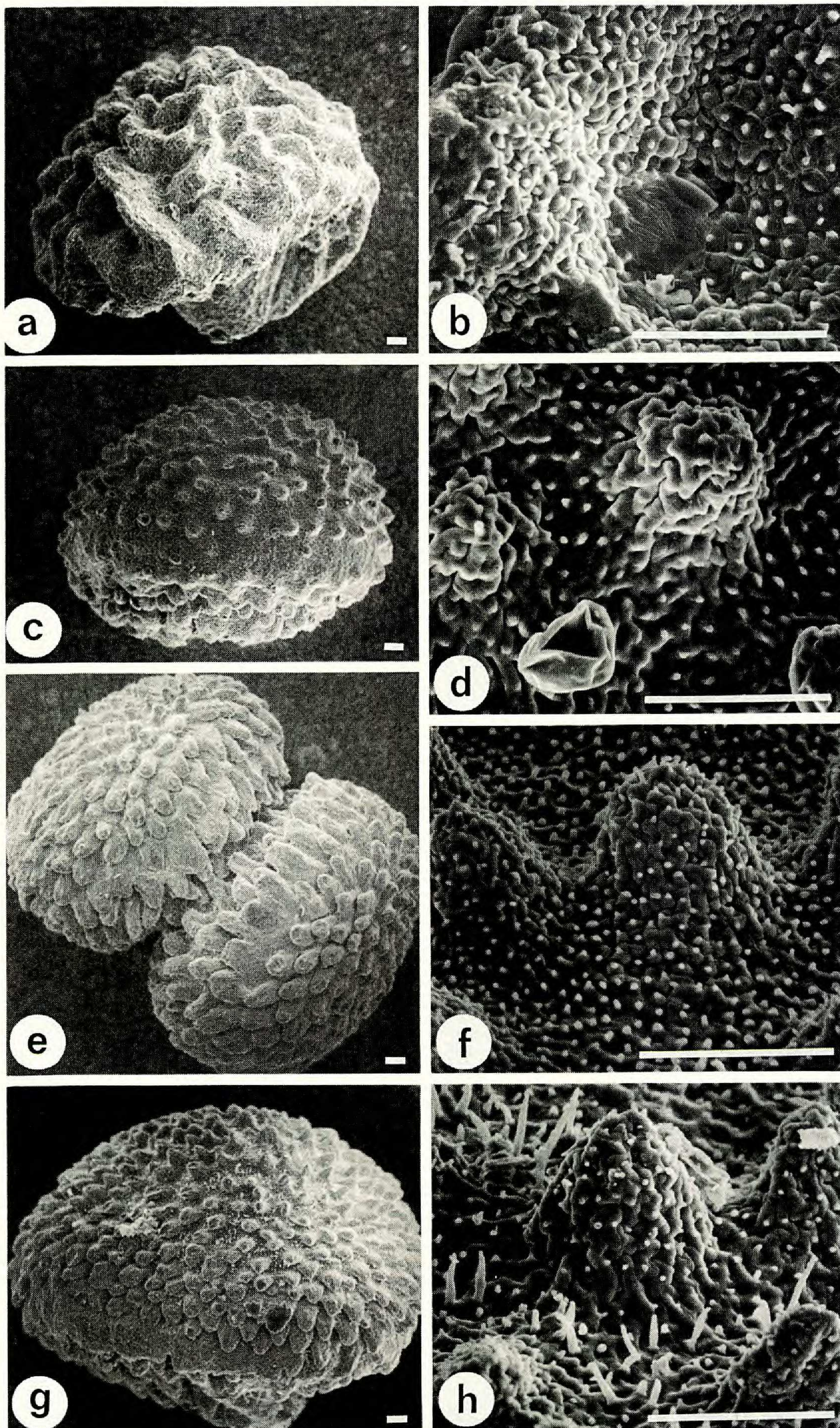


FIG. 2. Scanning electron micrographs of nutlets of *Scutellaria*. a–b. *S. tuberosa* (Olmstead 522): a. Lateral view of whole nutlet; b. Enlarged portion of nutlet surface showing nearly regular polygonal epidermal cells. c–d. *S. bolanderi* subsp. *austromontana* (Olmstead 803): c. Lateral view of whole nutlet; d. Enlarged portion of nutlet surface showing irregularly elongate epidermal cells and sessile glands. e–f. *S. angustifolia* subsp. *micrantha* (e, Olmstead 636; f, Olmstead 618): e. Dorsi-lateral view of two nutlets attached at the gynobase; f. Enlarged portion of nutlet surface. g–h. *S. angustifolia* subsp. *angustifolia* (Olmstead 551): g. Dorsi-lateral view of whole nutlet showing circumferential band consisting of coalescent papillae; h. Enlarged portion of nutlet surface. Scale bar=0.1 mm.

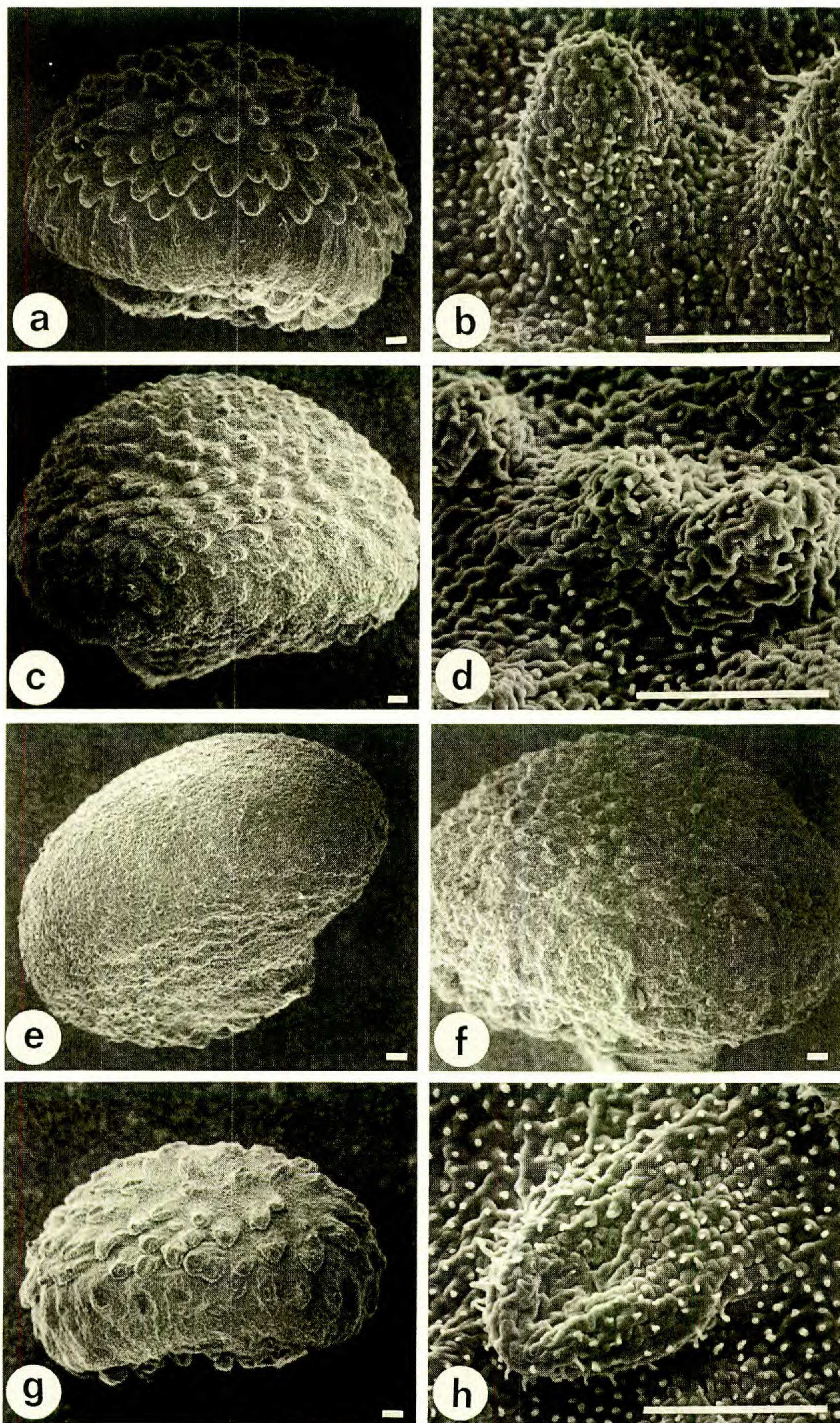


FIG. 3. Scanning electron micrographs of nutlets of *Scutellaria*. a-b. *S. antirrhinoides* (Olmstead 465): a. Dorsilateral view of whole nutlet; b. Enlarged portion of nutlet surface. c-e. *S. californica* (c-d, Olmstead 402; e, Olmstead 666): c. Dorsi-lateral view of whole nutlet; d. Enlarged portion of nutlet surface; e. Lateral view of whole nutlet showing nonpapillate form from Sonomo Co., California; f-h. *S. siphocampyloides* (f, Olmstead 438; g-h, Olmstead 813): f. Dorsilateral view of whole nutlet showing numerous sessile glands; g. Dorsi-lateral view of whole nutlet showing circumferential band marked by the absence of papillae; h. Enlarged portion of nutlet surface. Scale bar = 0.1 mm.

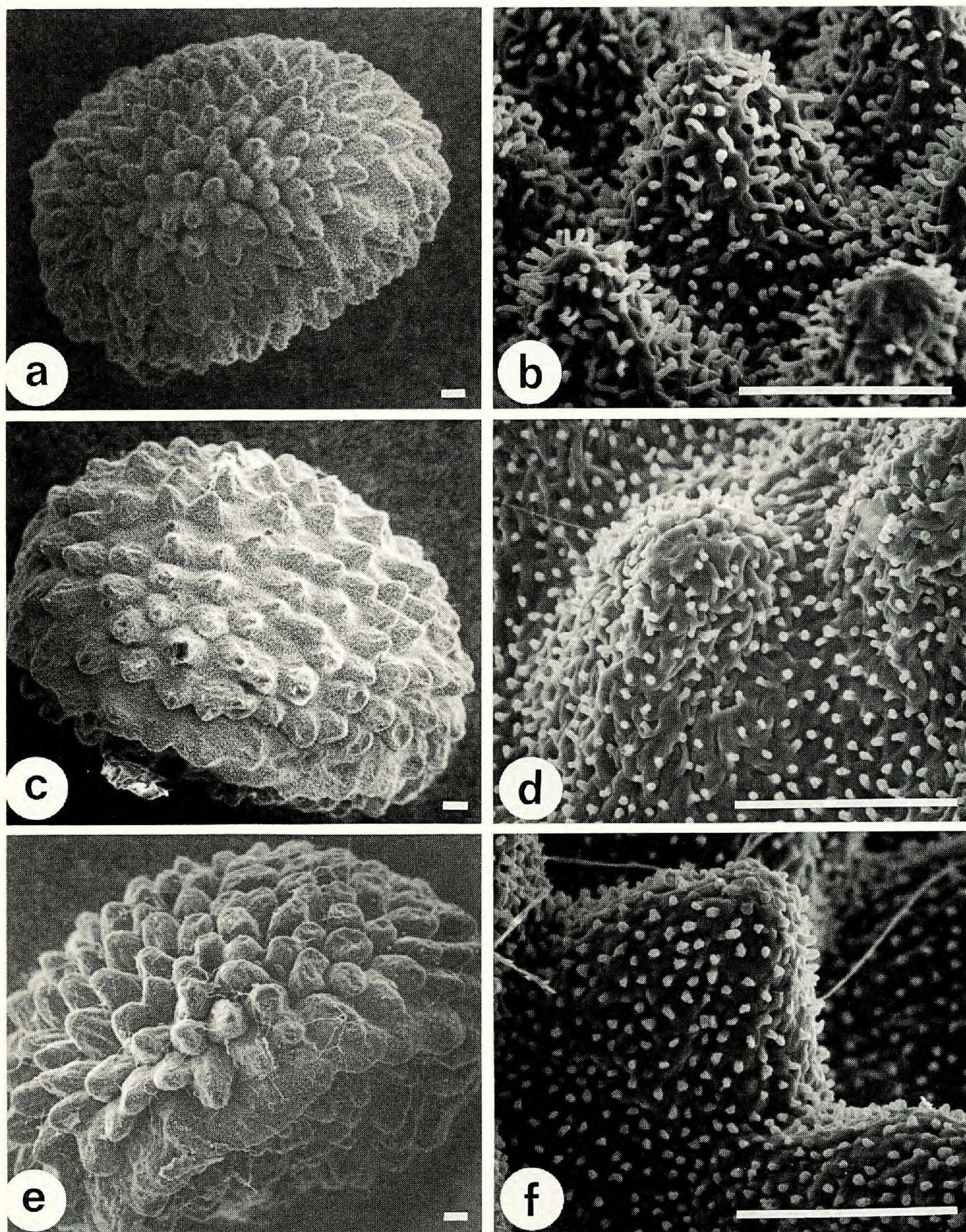


FIG. 4. Scanning electron micrographs of nutlets of *Scutellaria*. a–b. *S. nana* (Olmstead 588): a. Dorsal view of whole nutlet; b. Enlarged portion of nutlet surface showing the elongate, bulbous-tipped protuberances on the epidermal cells. c–d. *S. sapphirina* (Olmstead 596): c. Dorsi-lateral view of whole nutlet; d. Enlarged portion of nutlet surface. e–f. *S. brittonii* (Olmstead 642): e. Lateral view of whole nutlet; f. Enlarged portion of nutlet surface showing a large conical papilla. Scale bar = 0.1 mm.

Sessile glands appear on the nutlets of all species, although the nutlets may be eglandular in some populations. Mature nutlets are black in all species in the group, except *S. bolanderi*, in which they are usually brown or brown-grey, typically ovoid (to subglobose in *S. bolanderi* and turbinate in *S. tuberosa*), 1.1–2.0 mm long, and 1.0–2.0 mm wide. The nutlets may have a distinct circumferential band (*S. an-*

angustifolia, *S. antirrhinoides*, *S. bolanderi*, and *S. sapphirina*), may be polymorphic for circumferential bands (*S. brittonii*, *S. californica*, *S. nana*, and *S. siphocampyloides*), or lack circumferential bands entirely (*S. tuberosa*). The circumferential bands seem to be of two types. Typically they are formed by the coalescence of papillae (Fig. 2g); however, in *S. californica* and *S. siphocampyloides*, the absence of papillae around the midsection of the nutlets gives a banded appearance (Fig. 3g). The papillae are small and cylindrical to conical with rounded apices in *S. angustifolia*, *S. antirrhinoides*, *S. bolanderi*, *S. californica*, *S. nana*, *S. sapphirina*, and *S. siphocampyloides* (sometimes absent in *S. californica*), large and conical in *S. brittonii* (Figs. 4e–f), or large, irregularly shaped and often coalescent in *S. tuberosa* (Fig. 2a). The epidermal cells of the nutlets are irregularly elongate with a small terminal protuberance in most species of the *S. angustifolia* complex (Fig. 2d). However, in *S. tuberosa* the cells are nearly polygonal or hemispheric (Fig. 2b), rather than elongate, and in *S. nana* and *S. sapphirina* the apical protuberances on the epidermal cells are elongate and bulbous-tipped (Fig. 4b).

HABITATS AND PHENOLOGY

A great diversity of habitat specificities exists among species of the *Scutellaria angustifolia* complex. Habitat preferences range from moist streamside gravel to seeps and openings in pine-oak woodlands, sagebrush desert, and chaparral. All habitats share an element that is important to the ecology of the taxa in the group: all taxa live in summer-dry environments, in which summer drought imposes a period of dormancy. This tendency is most pronounced in *S. tuberosa*, of the California chaparral, in which the rhizomes are modified to form distinct tubers that must undergo an obligate period of dormancy before sprouting to form the next season's shoot. In all other species within the group, rhizomes may be induced to emerge at any time given sufficient moisture. The opposite extreme for the group is observed in *S. bolanderi*, which inhabits the margins of small streams, usually with intermittent flow, in the Sierra Nevada foothills and the mountains of southern California. In these circumstances the summer drought condition comes later in the season, or in some years may not come at all. This species is rarely found along larger streams with permanent stream flow.

Flowering phenology appears to be timed to moisture regime in the soil and varies from species to species (or from population to population within a species). In *S. tuberosa*, flowering occurs from late March to early May, whereas in *S. bolanderi* flowering does not begin until late June and extends through August. All other species in the *S. angustifolia* complex occupy habitats intermediate in the timing of moisture availability (if not amount) and exhibit intermediate flowering phenologies (late May–July). All taxa in the group initiate flowering when the soil begins to dry and often will be found at peak of flowering when the soil is bone dry. Variability within species in timing of flowering appears to be related to variation in water availability within a given plant community and is correlated with altitude or latitude, whereas differences between species are related to different basic moisture regimes in the plant communities to which they belong.

Variation in soil moisture appears to be the most important factor determining differences in habitat specificity in the group, although substrate preference also plays a role. The taxa from the Great Basin and Columbia River Basin, *S. angustifolia*, *S. nana*, and *S. sapphirina*, are restricted to basalt-derived substrates

(although *S. sapphirina* has been observed on alluvial soils of mixed origin). *Scutellaria brittonii* occurs primarily on coarse shallow soil of granitic origin along the Front Range of the Rockies. The California taxa, *S. antirrhinoides*, *S. bolanderi*, *S. californica*, *S. siphocampyloides*, and *S. tuberosa*, occur on a variety of substrates, including serpentine.

CHROMOSOME NUMBERS

Cytological material was obtained from root tips of plants that were collected in the field and grown in the greenhouse. The chromosomes were stained with acetocarmine according to the procedure of Soltis (1980). Mitotic chromosome counts were obtained for 22 populations representing all nine species. A count of $2n=22$ is reported for *S. brittonii* and counts of $2n=24$ are reported for all other taxa (appendix). Voucher specimens for the collections listed in the appendix are deposited in the University of Washington herbarium (WTU).

No previous chromosome counts for any members of the *Scutellaria angustifolia* complex are reported. The chromosome numbers reported here ($2n=22, 24$) are high enough that one may not assume a priori that they are diploid; however, experimental evidence from isozyme analyses indicates a gene number for soluble enzymes that is typical of diploids, with no evidence of polyploidy. Additionally, the isozyme analysis, which sampled a much larger number of populations than were sampled for direct counts of chromosome number, does not indicate any differences in ploidy among populations within any species of the group. Two small-flowered taxa of *Scutellaria* from eastern North America, *S. leonardii* and *S. parvula*, which were included in Epling's (1942) section *Galericularia*, have been reported (Gill 1981) to have $n=10$ chromosomes. Evidence from morphology and from the isozyme study of a limited number of individuals of these two taxa suggests that they may be derived from within the *S. angustifolia* complex (Olmstead 1989). The chromosome numbers reported here ($2n=22, 24$) further suggest that the derivation of these two taxa may have been accompanied by an aneuploid reduction in chromosome number.

Chromosome numbers from other species of *Scutellaria* (Collins 1976; Gill & Morton 1978; Gill 1981) show a considerable amount of variation within the genus in North America (appendix). The results reported for section *Annulatae* (Collins 1976) and this study of the *Scutellaria angustifolia* complex indicate a low degree of variability within groups and suggest that chromosome number may provide valuable phylogenetic information at the sectional level within the genus.

TAXONOMY

Scutellaria L., Sp. pl. 598. 1753.—TYPE: *Scutellaria galericulata* L.

Plants herbaceous or subshrubs, annual or perennial, perennating by tubers, rhizomes, stolons, or woody caudex. Flowers solitary in the axils of leaves or bracts or verticillate or in terminal or lateral racemes; calyx bilabiate, the lips equal, entire, rounded, with concave to subconical transverse crest or "scutellum" on upper lobe, enclosing the nutlets in fruit, dehiscent along lateral sutures, the upper lobe deciduous; corolla red, yellow, white, or dark to light violet, the lower lip variously mottled or plain, spreading or reflexed, the tube straight, recurved, or arcuate, the upper lip usually galeate; stamens four, in two pairs, enclosed by the

upper lip of the corolla, the filaments pilose, attached at or above the middle of the tube, the anthers of the lower pair with one fertile and one aborted anther sac, the anther sacs with cilia lining the suture; gynoeceum of four basally attached mericarps mounted on an elevated gynophore, the gynophore green, yellow, orange, or red and covered with small white sessile glands or naked. Nutlets ovoid to subglobose or turbinate, buff to black, with or without sessile glands, variously papillate or smooth, with or without a circumferential band.

THE SCUTELLARIA ANGUSTIFOLIA COMPLEX

Plants herbaceous, perennial, perennating by slender rhizomes swollen at the ends or tubers. Flowers solitary in leaf axils; calyx with concave transverse crest (subconical in *S. tuberosa*); corolla 12–35 mm long, white to ochroleucous to violet, the lower lip variously mottled or uniform, spreading or reflexed, the tube straight or recurved; gynophore green-yellow or orange-red. Nutlets brown or black, papillate, with or without circumferential band.

KEY TO THE SPECIES OF THE SCUTELLARIA ANGUSTIFOLIA COMPLEX

1. Corolla white to creamy-yellow, often with blue or purple markings on lower lip.
 2. Leaves crenate, cordate; plants pubescent with long (up to 2 mm) spreading multicellular hairs, sometimes with gland-tipped hairs; flowers white, the lower lip mottled with blue; plants 30–80 cm tall; streamsides in central and southern Sierra Nevada and mountains of southern California.
 3. Corollas 15–19 mm long; leaf length between 1–2 times the width; Sierra Nevada.

S. bolanderi subsp. *bolanderi*.
 3. Corollas 12–14 mm long; leaf length more than 2 times the width; San Bernardino Co. to San Diego Co.

S. bolanderi subsp. *austromontana*.
 2. Leaves, at least on upper part of stem, entire (if crenate, only on stem below first flowering node), ovate to oblong, or obovate; plants with short hairs 0.1–0.2 mm long, ascending or descending, and sometimes with gland-tipped hairs; plants 5–30 (–40) cm tall.
 4. Plants low-growing, tufted, 2–10 (–20) cm tall; stem hairs 0.1–0.2 mm long, descending or downcurled, sometimes with gland-tipped hairs 0.5–1.0 mm long; flowers ochroleucous (creamy-yellow), occasionally tinged with purple, the lower lip mottled with purple, glabrous, or with few, long, erect hairs; gynoeceal disk orange-red; leaves rhomboid to obovate; basalt substrates in sagebrush desert.

S. nana.
 4. Plants erect, 20–35 cm tall; stem hairs 0.1–0.2 mm long, ascending or upcurled, and usually with gland-tipped hairs 0.5–1.0 mm long; flowers white, occasionally tinged with pink or blue, without markings on lower lip; lower lip densely villous; gynoeceal disk green-yellow; leaves ovate to oblong; mixed conifer and pine-oak woodlands of northern California.

S. californica.
1. Corolla blue to violet-blue, often with white on lower lip.
 5. Leaves crenate; stems, leaves, and calyces with hairs 1.0–3.0 mm long; plants forming distinct tubers 0.5–2.0 cm long; chaparral and oak woodlands, northern Baja California to southwestern Oregon.

S. tuberosa.
 5. Leaves entire, at least on upper part of stem; stems, leaves, and calyces with short appressed hairs 0.1–0.2 mm long, and sometimes with gland-tipped hairs 0.5–1.0 mm long; plants forming elongate, swollen rhizomes constricted at the nodes.
 6. Corollas 22–35 mm long.
 7. Stem with hairs 0.1–0.2 mm long, descending or downcurled, sometimes with gland-tipped hairs 0.5–1.0 mm long (if both are present, see alternate lead); leaves with prominent veins abaxially; nutlets with large conical papillae; on coarse granitic soils along the Front Range of the Rocky Mountains.

S. brittonii.
 7. Stem with hairs 0.1–0.2 mm long, ascending, upcurled, or absent (rarely descending, then only on plants with capitate glands and from the inner South Coast Ranges of California), sometimes with gland-tipped hairs 0.5–1.0 mm long; leaves with shallow veins abaxially; nutlets with small cylindrical papillae; plants of the Great Basin, Columbia River Basin, and California.

8. Lower lip of corolla spreading or slightly reflexed, the upper lip \pm equal to lower lip; first flowering node 3–9 nodes above base of stem; leaf at first flowering node less than five times longer than wide; basal leaf margins entire; on basalt substrates in Great Basin and Columbia River Basin.
9. Corollas 22–35 mm long, usually with gland-tipped hairs; first flowering node 6–9 nodes above base of stem; ponderosa pine woodland and sagebrush grassland, northeastern Oregon, eastern Washington, and northern Idaho.
S. angustifolia subsp. *angustifolia*.
9. Corollas 12–22 mm long, usually without gland-tipped hairs; first flowering node 3–6 nodes above base of stem; sagebrush desert and margins of ponderosa pine woodland, northern Nevada, southeastern Oregon, and southern Idaho.
S. angustifolia subsp. *micrantha*.
8. Lower lip of corolla \pm strongly reflexed, upper lip = or > lower lip; first flowering node 8–12 nodes above base of stem; leaf at first flowering node five or more times longer than wide; basal leaf margins usually crenate; stems sometimes glabrous; on various substrates in California.
S. siphocampyloides.
6. Corollas 12–22 mm long.
10. Stem with hairs 0.1–0.2 mm long, descending or downcurved, never with gland-tipped hairs; leaves rhomboid to obovate; lower lip of corolla glabrous; plants usually with dwarf, tufted habit 5–10 (–20) cm tall (similar to *S. nana*); restricted to mountains of eastern Nevada (primarily White Pine Co.), and adjacent Utah.
S. sapphirina.
10. Stem with hairs 0.1–0.2 mm long, ascending or upcurved; sometimes with gland-tipped hairs 0.5–1.0 mm long; leaves ovate to oblong; lower lip of corolla usually pubescent; plants usually erect, branched or single-stemmed, 10–30 (–35) cm tall.
11. Lower lip of corolla \pm densely pilose with long erect hairs; first flowering node 5–9 nodes above base of stem; stems sometimes with gland-tipped hairs; basal leaf margins usually crenate; various substrates, northern California and Oregon west of the Cascade mountains.
S. antirrhinoides.
11. Lower lip of corolla sparsely pubescent or glabrous; first flowering node 3–6 nodes above base of stem; stem never with gland-tipped hairs; basal leaf margins entire; basalt substrates, northern Great Basin and Snake River plains.
S. angustifolia subsp. *micrantha*.

Scutellaria angustifolia Pursh, Fl. amer. sept. 412. 1814.—TYPE: USA. Idaho: Idaho Co., “On the Kooskooskee”, or Clearwater River, near Kamiah, 5 Jun 1806, *Lewis & Clark s.n.* (holotype: PH!).

Plants (5–) 10–30 (–35) cm tall, perennating by slender rhizomes swollen at the ends; stems single or branched near the base; stems and leaves moderately covered with trichomes 0.1–0.2 mm long and appressed-ascending, and rarely sparsely covered with gland-tipped trichomes. Basal leaves often turning red and then deciduous, with petioles 5–10 mm long; leaves below first flowering node short-petiolate to sessile, the blades ovate, entire, the apices rounded; leaves above first flowering node sessile, the blades ovate to oblong, entire, the apices rounded; leaf at first flowering node (10–) 15–25 (–35) mm long, (3.5–) 5–10 (–15) mm wide, mean length/width = 3.2. Flowers axillary, first appearing 3–9 nodes above base of stem and continuing up the stem; pedicels 3.0–7.0 mm long; calyx 3.0–5.0 mm long, with concave transverse crest on upper lobe; corolla violet-blue, 12–30 mm long, personate, the abaxial surface frequently with gland-tipped trichomes, the adaxial surface with long, tangled hairs, the lower lip with a white patch, a white patch mottled with violet, or uniformly violet-blue; filaments attached above the middle of the corolla tube; gynoecial disk green-yellow. Nutlets black, ovoid, 1.4–1.8 mm long, 1.2–1.6 mm wide, covered with small cylindrical papillae, surrounded by a distinct circumferential band, sparsely covered with sessile glands or eglandular. Chromosome number: $2n=24$. Figs. 1b, 2e,f,h, 5a–d, 7.

Scutellaria angustifolia is morphologically and ecologically the most variable taxon in the group. This species is found in ponderosa pine woodlands of eastern Oregon, Washington, and Idaho, as well as in the sagebrush desert of southeastern Oregon, northern Nevada, and southern Idaho. Variation in a suite of morphological characters suggests the recognition of two subspecies, *S. angustifolia* subsp. *angustifolia* and *S. angustifolia* subsp. *micrantha*. Subspecies *angustifolia* is distributed primarily in ponderosa pine woodlands in the northern part of the range. In contrast to subsp. *micrantha*, it is characterized by longer and narrower leaves, longer pedicels, larger flowers, and a longer period of vegetative growth, measured in number of leaf nodes before flower initiation. Subspecies *micrantha* is distributed primarily in the sagebrush desert in the southern part of the range. It has shorter, broader leaves, shorter pedicels, smaller flowers, and becomes reproductive at an earlier stage of development than subsp. *angustifolia*. This set of character differences between subspecies appears to represent modification to the environmental differences of their respective habitats, specifically moisture availability.

The remarkable differences between the morphological extremes in this species has led previous workers to recognize two species: the large-flowered plants belonging to *S. angustifolia* and the small-flowered plants belonging to *S. antirrhinoides*. The inclusion of the small-flowered plants from the Great Basin in *S. antirrhinoides* was based on similarities in floral and vegetative morphology, but did not consider characteristics of those plants shared with the large-flowered *S. angustifolia* sensu stricto. These characteristics include: lower lip of the corolla without dense long hairs, basal leaves with entire margins, habitats restricted to basalt substrates, and distributional contiguity. Along the zone of contact between the ponderosa pine woodland and sagebrush desert in central Oregon and central Idaho, plants are found with morphological characteristics intermediate between the two extremes represented by subsp. *angustifolia* and subsp. *micrantha*. Experimental evidence from isozyme analysis confirms the conspecific relationship of these two taxa. Populations of the two subspecies have a genetic similarity (Nei 1978) of 0.91 and have the same allele at highest frequency in all 18 isozyme loci surveyed, whereas the genetic similarity between populations of subsp. *micrantha* and *S. antirrhinoides* is only 0.74; the two taxa have different alleles at highest frequency in several loci (Olmstead 1989). *Scutellaria angustifolia* subsp. *micrantha* can be distinguished morphologically from *S. antirrhinoides* by the lack of hairs on the lower lip of the corolla, entire leaf margins on the basal leaves, and by having its first flowering node 3–5 nodes above the base of the stem vs. 6–9 nodes above the base for *S. antirrhinoides*.

Collections attributable to *S. angustifolia* subsp. *micrantha* from the Wasatch Mountains of Utah may represent the remnants of a distribution that once encircled the former Lake Bonneville.

***Scutellaria angustifolia* subsp. *angustifolia*.**

Scutellaria veronicifolia Rydberg, Bull. Torrey Bot. Club 36: 681. 1909.—TYPE: USA. Idaho: Nez Perce Co., valley of Peter Creek, 4 May 1892, Sandberg, MacDougall & Heller 115 (holotype: NY!; isotypes: GH! NY! US!).

Leaves 3–5 times as long as wide. Flowers first appearing 6–9 nodes above base of stem; pedicels 4–8 mm long; corollas 22–35 mm long, covered abaxially with gland-tipped trichomes. Figs. 1b, 2e,h, 5a–d.

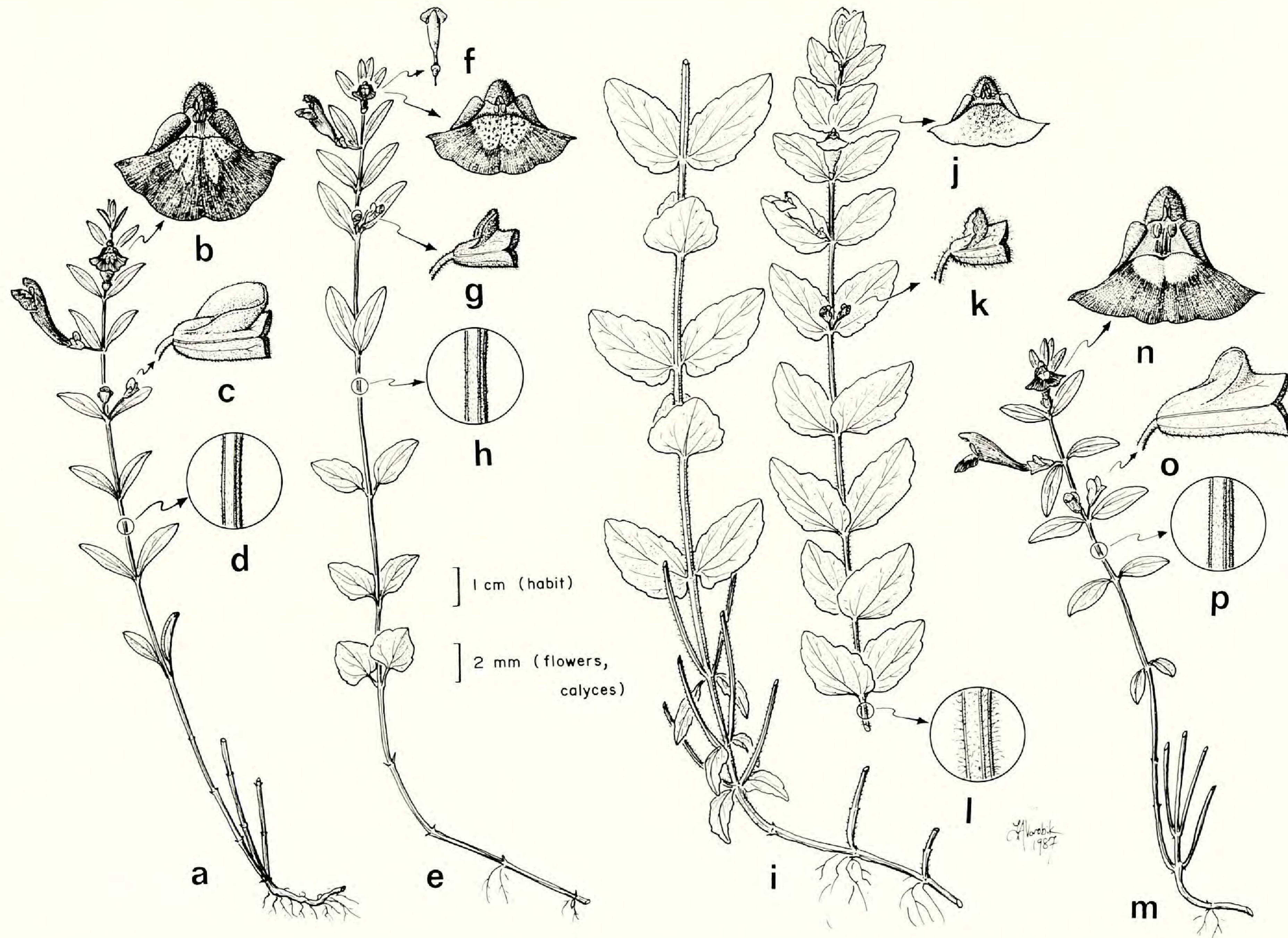


FIG. 5. *Scutellaria angustifolia* subsp. *angustifolia*, *S. antirrhinoides*, *S. bolanderi* subsp. *bolanderi*, and *S. brittonii*. a–d. *S. angustifolia* subsp. *angustifolia* (from Olmstead 638). a. Habit. b. Corolla. c. Calyx. d. Stem with trichomes. e–h. *S. antirrhinoides* (from Olmstead 452). e. Habit. f. Corolla. g. Calyx. h. Stem with trichomes. i–l. *S. bolanderi* subsp. *bolanderi* (from Olmstead 386). i. Habit. j. Corolla. k. Calyx. l. Stem with trichomes. m–p. *S. brittonii* (from Clements 95). m. Habit. n. Corolla. o. Calyx. p. Stem with trichomes.

Phenology. Flowering May–July.

Distribution (Fig. 6). East slope of the Cascades in Oregon and the east end of the Columbia River Gorge east across the northern half of Oregon, in central Idaho primarily along the Snake, Salmon, and Clearwater Rivers, north in Idaho and

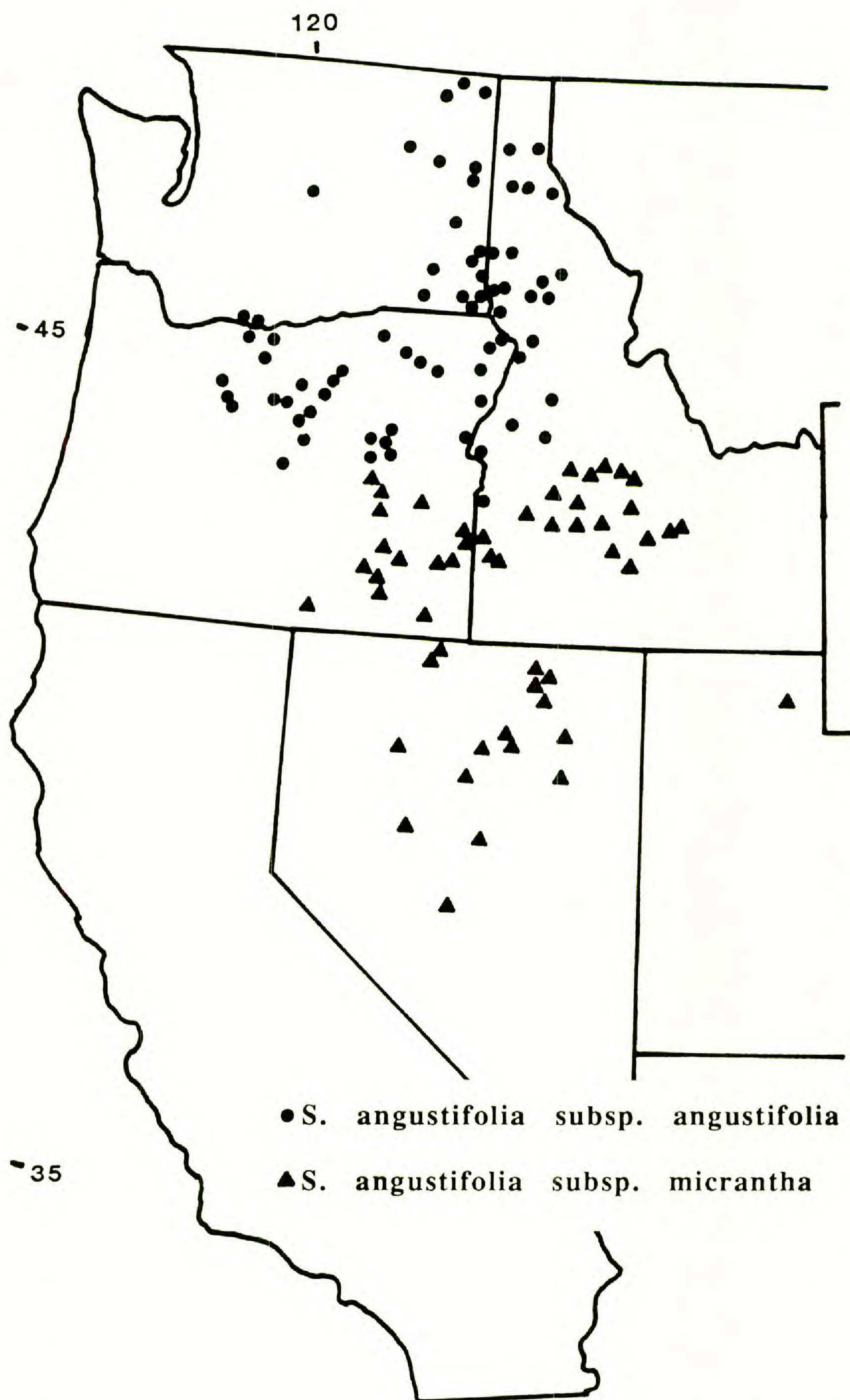


FIG. 6. Distribution of *Scutellaria angustifolia* subsp. *angustifolia* and *S. angustifolia* subsp. *micrantha*.

eastern Washington to the Canadian border, with one collection known from adjacent British Columbia; predominantly on basalt derived substrate in openings in ponderosa pine woodland and on basalt scree slopes along the Columbia River and its tributaries; 200–1750 m.

REPRESENTATIVE SPECIMENS: IDAHO. Adams Co.: 20 mi S of New Meadows near hwy to Weiser, *Hitchcock & Muhlick* 13865 (DS, MO, NY, UC, WTU). Bonner Co.: along Pend Oreille River, 4 mi E of Priest River, *Baker* 8969 (NY, WTU); 10 mi E of Newport near Hwy 2, *Hitchcock* 17649 (NY, UC, WTU); Hope, Jul 1929, *Epling s.n.* (LA). Canyon Co.: Big Willow, *MacBride* 104 (GH, NY, UC, US, WTU). Clearwater Co.: 5 mi NW of Orofino on rd to Kendrick, *Olmstead* 552 (UC, WTU); "Clearwater", *Spalding s.n.* (GH); Greer, *Christ* 7486 (NY); near Pierce, *Cook s.n.* (WIS). Idaho Co.: Kamiah, across river from town, *Olmstead* 553 (CAS, WTU); Divide Cr, near Snake River, *Packard* 414 (UC); Snake River canyon at Willow Cr, 2 mi N of Sheep Cr, *Constance et al.* 1581 (GH, MICH, MO, UC, WTU); Kamiah, *Constance et al.* 1119 (GH, NY, US, WTU); Salmon River canyon, 5 mi S of White Bird, *Hitchcock & Muhlick* 8484 (NY, WTU). Kootenai Co.: Coeur d'Alene, *Leiberg* 1548 (GH, NY, UC, US); Hwy 10 E of Coeur d'Alene, *Call* 341 (NY). Latah Co.: head of Hatwai Canyon between Uniontown and Lewiston, *Cronquist* 5790 (MICH, NY, UC, US, WTU); Moscow, *Abrams* 710 (UC); Deary, *Murley* 176 (NY); Troy, *Jardine* 256 (US). Lewis Co.: 3 mi N of Ferdinand, *Christ* 10982. Nez Perce Co.: 2 mi E of Lewiston, on the N side of the Clearwater River, *Weber* 2131 (WTU); along Hwy 95, 1 mi N of Hwy 12, 2 mi NE of Lewiston, *Olmstead* 557 (RENO, WTU); Hwy 12, ca 5 mi E of Lewiston, *Olmstead* 555 (CAS, WTU); Lewiston, *Heller* 3150 (NY, PH, UC, US). Shoshone Co.: Kellogg, *Christ* 3350 (NY). Valley Co.: 5 mi E of Cascade, *Hitchcock & Muhlick* 13987 (MO, NY, UC, WTU); 9 mi E of McCall, *Holmgren & Tillett* 9531 (CAS, GH, NY, OSC, UC, WTU). Washington Co.: Olds Ferry on Union Pacific R.R., *Christ* 9394 (NY).—WASHINGTON. Asotin Co.: 3 mi S of Asotin, *Hitchcock & Muhlick* 8381 (GH, NY, UC, US, WTU); Grande Ronde River at mouth of Cottonwood Cr, SW of Anatone, *Cronquist* 5738 (GH, MICH, NY, TEX, UC, WTU); Couse Canyon, 3 mi W of Snake River, *Hitchcock* 23481 (NY, UC, WTU). Chelan Co.: bank of Columbia, Wenatchee, *Whited* 1378 (OSC). Columbia Co.: Columbia River, below mouth of Colockum Cr., *Davis* 201 (WTU). Ferry Co.: San Poil River, 1 mi N of Keller Ferry, *Rogers* 479 (GH, LA, NY, UC, WIS, WTU). Garfield Co.: Blue Mts, first ridge N of Cape Horn Mt, near Big Mud trail, *Peters* 351 (UC). Klickitat Co.: 4 mi E of Lyle on Hwy 14, *Olmstead* 300, 561 (UC, WTU); Bingen, *Suksdorf* 6577 (DS, GH, NY); western Klickitat Co., *Suksdorf s.n.* (NY, PH). Pend Oreille Co.: near Metaline, *Thompson* 9223 (GH, NY, UC, US, WTU). Spokane Co.: Clarks Springs, 10 mi N of Spokane, *Beattie & Chapman* 2020 (UC, US); Spokane, *Kraeger* 10 (GH, NY, UC, US, WTU); Spokane, *Henderson s.n.* (WTU). Stevens Co.: Spokane River 13 mi above its mouth, *Rogers* 484 (GH, LA, NY, UC, WIS); Northport, *Hedgecock s.n.* (WTU); 6.5 mi NE of Marcus, *Hedgecock s.n.* (NY, WTU). Walla Walla Co.: Waitsburg, *Horner* R178B411 (GH, US). Whitman Co.: along Snake River between Wawawai and Clarkston, *Olmstead* 558, 559 (CAS, NY, UC, US, WIS, WTU); Rock Lake, *Beattie & Lawrence* 2339 (PH, UC); Pullman, *Piper* 1570, 1571 (GH, NY, UC, US, WTU); Snake River near Clarkston, *Constance et al.* 1053 (GH, LA, NY, OSC, PH, UC, US, WIS, WTU); Pullman, *Hughes s.n.* (UC); Pullman, *Elmer* 181 (NY, US).—OREGON. Baker Co.: near Halfway, *Gustafson* 35 (OSC, UC, WTU); talus slide above Burnt River, 1.5 mi NE of Huntington, *Hitchcock & Muhlick* 20995 (NY, WTU). Crook Co.: Maury Mts, along Forest Hwy 17, 3–5 mi S of Hwy 380, *Olmstead* 700, 702 (WTU); Blue Mts, *Eggleston* 11381, 11383 (US); Ochoco Mts, near Indian Cr, just N of Big Summit Prairie, between Prineville and Mitchell, *Cronquist* 7487. Grant Co.: along Silvies River near Hwy 395, S of Seneca, *Olmstead* 330, 637 (WTU); along Strawberry Cr rd, S of Prairie City, *Olmstead* 323, 325, 327 (CAS, OSC, UC, WTU); Vance Cr rest area, Hwy 395, ca 10 mi S of John Day, *Olmstead* 329 (OSC, WTU); Trout Farm campground, ca 12 mi S of Prairie City, *Olmstead* 321 (WTU); along S Fork John Day River, 8 mi S of Dayville, *Cronquist* 7011 (GH, NY, UC, WTU). Jefferson Co.: Rajneeshpuram (Big Muddy ranch), S of Antelope near rd to Mitchell, *Olmstead* 492, 499, 500 (OSC, WTU); Deschutes River near Madras, *Peck* 15799 (OSC, WTU); Warm Springs, *Murphey* 75 (OSC). Morrow Co.: along rd to Bull Prairie Lake, near Hwy 207, *Olmstead* 312 (OSC, WTU); Anson Wright Memorial Park, 5 mi S of Hardman, *Olmstead* 301, 302 (OSC, WTU); "Hati Hill," 0.5 mi NE of Anson Wright Co. Park, on Hwy 207, *Hunn* 455 (WTU). Sherman Co.: Shearers Grade rd, Deschutes canyon, *Baker* 774 (OSC); DeMoss Springs, *Peck* 9950 (LA, NY, OSC). Umatilla Co.: Pendleton, *Henderson* 99, 813 (GH, OSC, UC, US); Kamala, *Thompson* 4766 (US). Union Co.: Union, *Cusick* 75 (GH); La Grande, Beaver Cr, *Hansen* 1067 (WIS). Wallawa Co.: Enterprise, *Gilkey s.n.* (OSC); 4 mi NE of Buckhorn Springs, *Peck* 18298 (NY, OSC); rocky promontories along grade between Illahee Forest Service Camp and Skookum Cr, *Kruckeberg* 2341 (NY, UC, WTU); Snake River canyon, near mouth of Deep Cr, *Constance et al.* 1571 (OSC,

WTU). Wasco Co.: 12 mi S of Antelope on rd to Mitchell, *Olmstead 501* (OSC, WTU); Warm Springs Indian Res., *Gorman 5785* (UC); The Dalles, *Wilson s.n.* (GH); Dalles, *Kellogg & Harford 742* (GH, MO, NY, US); 1 mi N of Dufer, *Peck 14913* (OSC, PH). Wheeler Co.: 5 mi W of Mitchell on Hwy 26, *Olmstead 318* (OSC, WTU); along Hwy 207, 12 mi N of Mitchell, *Olmstead 315* (WTU); Fairview campground and along Hwy 207 to the S, 16 mi N of Spray, *Olmstead 314, 638, 640A-D* (CAS, NY, OSC, UC, US, WIS, WTU); W of Fossil, *Lawrence 438* (OSC, US); talus above John Day River, 13 mi W of Spray, *Cronquist 6436* (GH, NY, OSC, WTU); 4 mi W of Fossil, *Cronquist 6661* (GH, NY, OSC, WTU); near summit of grade, 7 mi E of Mitchell on Hwy 28, *Kruckeberg 2176* (NY, UC, WTU).—CANADA. BRITISH COLUMBIA. Pend Oreille River, *Macoun 67* (NY).

Scutellaria angustifolia* subsp. *micrantha Olmstead, subsp. nov.—TYPE: USA. Nevada: Elko Co., Ruby Mtns, Lamoille Canyon, 23.5 mi SE of Elko, 0.3 mi W of scout camp entrance, T32N, R58E, Sec. 9, 6920 ft, 3 Jul 1984, *Olmstead 620* (holotype: WTU!; isotypes: CAS! NY! OSC! UC! US!).

Scutellaria nevadensis Eastwood, Bull. Torrey Bot. Club 30: 492. 1903.—TYPE: USA. Nevada: Elko Co., Little Lakes Canyon, W Stampede, 1 Jul 1902, *Kennedy 546* (lectotype, designated by Epling, 1942; CAS!; isolectotypes: NY! US!).

Folia duplo usque ad triplo longiora quam latiora; flores primum evoluti in 3–6 nodi super basim caulis; pedicelli 2–4 mm longi; corolla 12–22 mm longa, raro trichomatibus glandiferis abaxialibus instructa.

Leaves 2–3 times as long as wide. Flowers first appearing 3–6 nodes above base of stem; pedicels 2–4 mm long; corollas 12–22 mm long, rarely with gland-tipped trichomes abaxially. Figs. 2e–f, 7.

Phenology. Flowering May–July.

Distribution (Fig. 6). Northern Great Basin in Nevada and southeastern Oregon eastward across the Snake River plains to central Idaho, with outlying collections attributable to this taxon from the foothills of the Wasatch Mts of Utah; basalt-derived substrate in sagebrush grassland of the Great Basin and Snake River plains and occasionally in open ponderosa pine woodland in central Idaho; 800–2500 m.

REPRESENTATIVE SPECIMENS: OREGON. Grant Co.: Silvies Lodge area, ca 35 mi N of Burns, *Steward 7133* (GH, PH, OSC, WTU); Strawberry Mt, *Denton 3203* (MICH, NY, OSC, WTU); Harney Co.: near Silvies River, 1 mi W of Silvies Ranch on USFS Rd 1880, 1.7 mi W of Hwy 395, 20 mi S of Seneca, *Olmstead 331, 636* (OSC, RENO, UC, WTU); Hwy 395, 16 mi N of Burns at stone monument, *Olmstead 333, 635* (CAS, WTU); Devine Canyon, Hwy 395, ca 13 mi N of Burns, *Olmstead 337* (OSC, WTU); 5 mi S of Princeton jct on rd to Diamond Craters, *Olmstead 348, 634* (NY, OSC, UC, WTU); Page Spring campground, 3 mi E of Frenchglen, *Olmstead 351, 709, 710* (OSC, WTU); Steens Mt, 9.6 mi from Frenchglen on rd to Fish Lake, *Olmstead 715* (WTU); roadside spring 15 mi N of Burns, *Thompson 12000* (CAS, DS, NY, US, WTU); margin of Ten Cent Lake, *Peck 21849a* (OSC); Stein's Mt, near Juniper ranch, *Train s.n.* (OSC). Lake Co.: canyon W of Adel, *Ripley & Barneby 6054* (CAS). Malheur Co.: Succor Cr rd near jct with Hwy 95, 18.4 mi N of Jordan Valley, *Olmstead 733a* (WTU); 4.4 mi N of Rockville on rd to Succor Cr Rec area, *Olmstead 733* (WTU); 6.9 mi N of Danner on rd to Cow Lake, *Olmstead 729* (WTU); Succor Cr area 19 mi NNW of Sheaville, *Holmgren & Holmgren 9273* (WTU); 1.5 mi E of Juntura, *Cronquist 8152* (CAS, DS, GH, NY, MICH, OSC, TEX, UC, WTU); 10 mi NE of Rome, *Peck 25763* (OSC, UC); Juniper Springs, *Leiberg 2260* (GH, NY, UC, US); 15 mi N of McDermitt, *Peck 21717* (OSC); Three Rocks Canyon, Owyhee River, *Dean 27* (OSC).—NEVADA. Churchill Co.: Clan Alpine Mts, near Cherry Cr rd, *Mozingo 76-46* (NY). Elko Co.: Bull Run Mts, 0.7 mi N of Maggie Summit, 9.6 mi SW of Hwy 225, *Olmstead 629* (NY, RENO, UC, WTU); Bull Run Mts, S of Maggie Summit, 0.3 mi N of Deep Cr jct, ca 62 mi N of Elko, *Olmstead 625* (CAS, US, WTU); Wild Horse Range, Owyhee River canyon, along Hwy 225, 1 mi N of Wild Horse Dam, *Olmstead 630* (CAS, US, WTU); Independence Mts, Jack Cr between Jack Cr ranch and Jack Cr summit, *Olmstead 622, 624* (CAS, NY, RENO, UC, US, WIS, WTU); Ruby Mts, Lamoille Canyon, 0.3 mi above scout camp

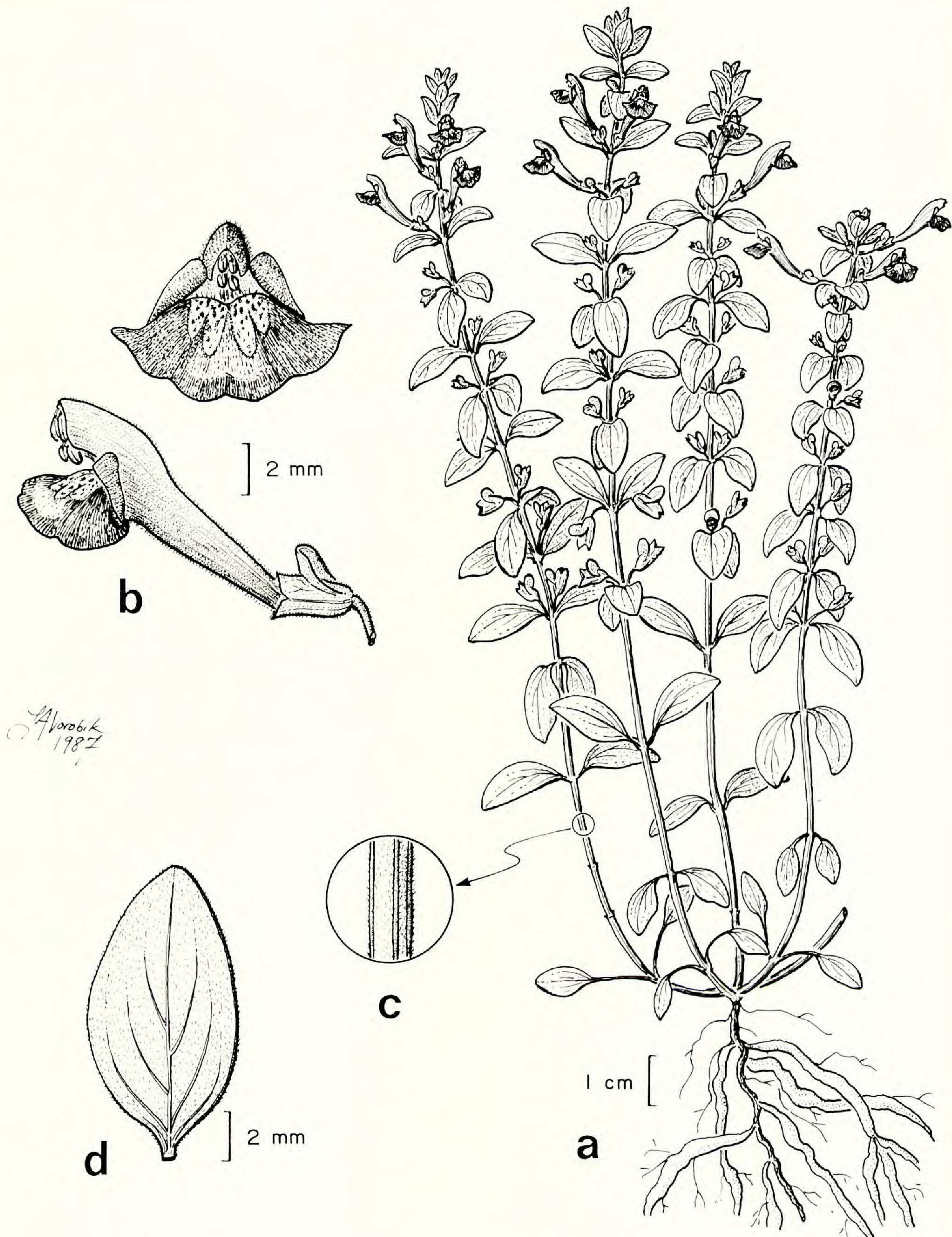


FIG. 7. *S. angustifolia* subsp. *micrantha*. a. Habit. b. Corolla. c. Stem with trichomes. d. Leaf. (from Olmstead 620).

entrance, *Olmstead* 620 (NY, OSC, UC, US, WTU); Ruby Mts, 5.6 mi W of Harrison Pass, 41 mi S of Elko, *Olmstead* 618 (NY, RENO, UC, WTU); W side of Independence Mts, 4.5 mi N of Stampede Ranch, T38N, R52E, S11, *Tiehm* 6110 (CAS, MO, NY); near Blaine P.O., *Heller* 11120 (DS, GH, MO, NY, PH, UC, US); Little Lakes Canyon, W Stampede, *Kennedy* 502 (DS, RM). Eureka Co.: Palisade exit to I-80, 0.7 mi E of Emigrant Pass, 31.5 mi W of Elko, *Olmstead* 631 (NY, UC, WTU); Emigrant Pass, Tuscarora Mts, *Mason* 4630 (NY, WTU); Palisade, *M. E. Jones* 4036 (CAS, DS, MO, NY, UC, US, WTU). Humboldt Co.: Santa Rosa Mts, 0.5 mi S of Hinkey summit, 14.4 mi N of Paradise,

Olmstead 632 (CAS, RENO, WIS, WTU); Santa Rosa Mts, *Gentry* 1572 (GH, NY, OSC, PH, TEX, UC, WTU); Santa Rosa Mts, Singas Cr, *Maguire & Holmgren* 22491 (GH, NY, UC, US, WTU). Lander Co.: 8–23 mi S of Battle Mountain, *Goodner & Henning* 940 (UC); Underwood Canyon, 7 mi S of Gund Ranch Exper. Sta., *Lott* 241 (MO, NY); 6 mi NE of Izzenhood ranch, *Holmgren* 539 (NY, OSC, UC). Nye Co.: Poplar branch of Pea Vine Cr, 7.2 mi above Pea Vine campground, *White & Neese* 257 (NY). Pershing Co.: Star Cr, southern Humboldt range, *Alexander & Kellogg* 4610 (DS, UC, US); Star Cr, E side of Star Peak, *Ownbey & Ownbey* 2880 (WTU). Locale uncertain: Havalick Mts, *Watson* 834 (GH, NY, US); “Nevada”, *Wheeler s.n.* (GH, US).—IDAHO. Ada Co.: Boise, *Clark* 140 (DS, GH, MO, UC, US). Blaine Co.: Lava Lake Craters, *Davis* 789 (LA, UC); Ketchum, *Nelson & Macbride* 1208 (DS, GH, MO, NY, UC, US, WTU); Picabo, *MacBride & Payson* 3005 (CAS, DS, GH, MO, NY, UC, US). Boise Co.: 1 mi N of Big Meadows, headwaters of S Fork Payette River above Sacajawea Hot Springs, *Hitchcock & Muhlick* 9881 (CAS, NY, UC, WTU); S fork Payette River, 1 mi E of Lowman on Hwy 21, *Elvander* 646 (WTU); Hwy 21, between Idaho City and Moore’s Cr summit, *Ertter* 2475. Butte Co.: NE of Martin, *Pennell* 20623 (PH); along hwy between Craters Of The Moon and Picabo, *Cronquist* 2399 (GH, MO); Craters Of The Moon, *Cronquist* 1179 (NY), *Davis s.n.* (NY). Camas Co.: 1 mi E of Carriatown, *Baker* 11115 (NY, WTU); Little Sandy River, 26 mi SE of Featherville, *Christ* 17471 (NY). Custer Co.: Robinson Bar, *Davis* 469 (LA); 2–3 mi below Stanley, *Cronquist* 2898 (GH, MO); 12 mi NE of Stanley on rd to Challis, *Hitchcock & Muhlick* 9596 (CAS, NY, UC, WTU). Elmore Co.: 4 mi N of Pine, N of Dog Cr, *Hitchcock & Muhlick* 8702 (CAS, DS, GH, MO, NY, PH, UC, WTU); 1 mi W of Atlanta, *Simpson* 150 (WTU); 4 mi NE of Anderson ranch on rd to Pine, *Christ* 17400 (OSC, NY); Jackass Cr, 2 mi E of Arrow Rock Reservoir, *Hitchcock* 15464 (NY, UC, WTU). Gooding Co.: 25 mi NW of Gooding, *Christ* 12358 (NY). Lincoln Co.: Shoshone, *Saunders* 4882 (MO). Owyhee Co.: Silver City, *Macbride* 937, 1689 (DS, GH, MO, NY, UC, US); Jump Cr, 6 mi NE of Oregon-Idaho line along Hwy 95, *Maguire & Holmgren* 26371 (DS, NY, UC, US, WTU); Twilight Gulch, *Maguire* 482 (DS, GH, MO, NY, UC, US, WTU); Owyhee Mts, *Mulford s.n.* (GH, MO, NY); Owyhee Mts, Twilight Gulch, near Silver City, *Munz* 14544 (DS, LA, UC).—UTAH. Weber Co.: Huntsville, *McKay s.n.* (GH, NY). Locale uncertain: Petersen Canon, Petersen, Utah, *Pammel & Blackwood* 3778 (?); “Utah Territory”, *Hayden Survey s.n.* (NY, PH).

Scutellaria antirrhinoides Benth., Bot. Reg. 18: pl. 1493. 1832.—TYPE: USA. Oregon or Washington: “Fort Vancouver, N.W. coast of N. America” [probably along Columbia River near Vancouver, Washington], *Scouler s.n.* (holotype: K!; isotype: NY!).

Scutellaria sanhedrensis Heller, Muhlenbergia 1: 31. 1904. *Scutellaria antirrhinoides* var. *sanhedrensis* (Heller) Leonard, Contrib. U.S. Natl. Herb. 22: 732. 1927.—TYPE: USA. California: about Summit Lake, near the summit of Mt. Sanhedrin, Lake County, 15 Jul 1902, *Heller* 5894 (holotype: BKL; isotypes: DS! GH! MO! NY! RM! US!).

Scutellaria viarum Heller, Muhlenbergia 1: 32. 1904.—TYPE: USA. California: west of Windsor near Russian River, Sonoma County, 27 Jun 1902, *Heller* 5786 (holotype: BKL!; isotypes: DS! GH! MO! NY! PH! US!).

Plants (5–) 10–25 (–35) cm tall, perennating by slender rhizomes swollen at the ends; stems single or branched near the base; stems and leaves moderately covered with trichomes 0.1–0.2 mm long and appressed-ascending, and occasionally sparsely covered with gland-tipped trichomes. Basal leaves often turning red and then deciduous, with petioles 5–10 mm long; leaves below first flowering node short-petiolate to subsessile, the blades ovate, entire or slightly crenate, the apices rounded; leaves above first flowering node subsessile, the blades ovate to oblong, entire, the apices rounded; leaf at first flowering node (10–) 15–25 (–30) mm long, 5–10 mm wide, mean length/width = 2.9. Flowers axillary, first appearing 5–9 nodes above base of stem and continuing up the stem; pedicels 3.0–4.5 mm long; calyx 3.0–4.0 mm long, with concave transverse crest on upper lobe; corolla violet-blue, 13–21 mm long, personate, short-pubescent abaxially, pilose with long, tangled hairs adaxially, with

scattered, long trichomes on the palate, the lower lip with a white patch mottled with violet; filaments attached above the middle of the corolla tube; gynoecial disk green-yellow. Nutlets black, ovoid, 1.5–1.8 mm long, 1.2–1.5 mm wide, covered with small cylindrical papillae, surrounded by a distinct circumferential band, sparsely covered with sessile glands. Chromosome number: $2n=24$. Figs. 3a,b, 5e–h.

Phenology. Flowering May–July.

Distribution (Fig. 8). Coast ranges of northern California from Sonoma and Lake counties northward, the foothills of the northern end of the Sierra Nevada, the Siskiyou-Klamath mountains, and northward in the foothills of the Cascades and coast ranges of Oregon to the Columbia River; openings in mixed conifer and pine-oak woodlands, primarily on dry rocky slopes and ridges, often on serpentine; 100–2000 m.

Scutellaria antirrhinoides is vegetatively similar to *S. californica*, *S. angustifolia*, and *S. siphocampyloides*, but can be distinguished from *S. californica* by the white corolla of the latter and from *S. angustifolia* subsp. *angustifolia* and *S. siphocampyloides* by the longer corollas of these two blue-flowered taxa. Morphologically, *S. antirrhinoides* resembles *S. angustifolia* subsp. *micrantha* very closely (see discussion of *S. angustifolia*), hence their former treatment as one species. However, the two taxa have disjunct distributions and distinct habitat preferences (*S. antirrhinoides* in conifer and oak woodlands on a variety of substrates; *S. an-*

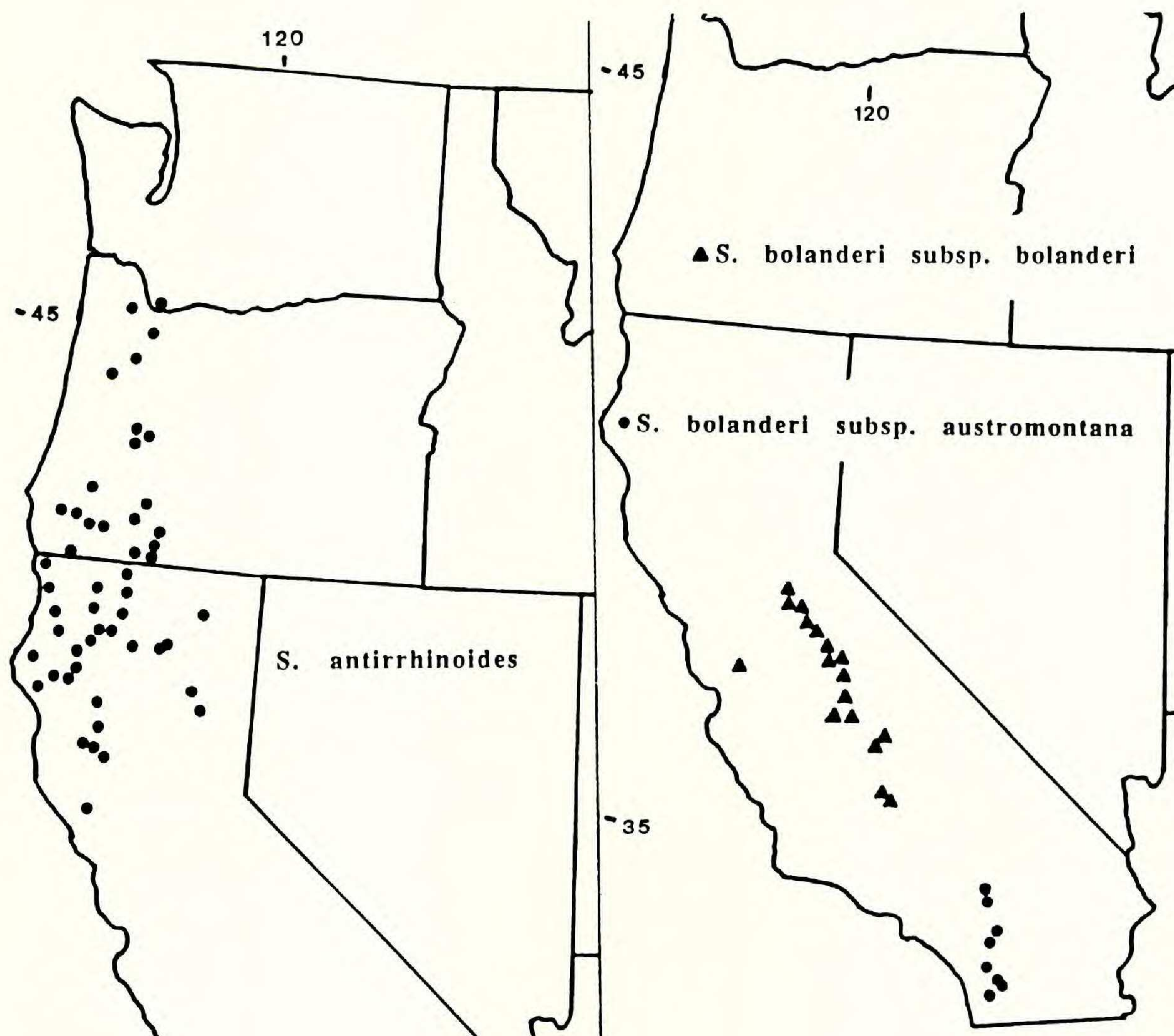


FIG. 8. Distribution of *S. antirrhinoides*, *S. bolanderi* subsp. *bolanderi*, and *S. bolanderi* subsp. *austromontana*.

gustifolia subsp. *micrantha* in sagebrush desert and nearly always on basalt derived substrates). The phylogenetic analysis of the *S. angustifolia* complex (Olmstead 1989) suggests that *S. antirrhinoides* retains the morphology that is ancestral to that of all of the taxa cited above.

Scutellaria antirrhinoides typically is found on drier sites than are other species of *Scutellaria* within its geographic range. It is known to occur on and off serpentine (a "Bodenvag" species, Kruckeberg 1984) and seems to do best in rocky open places where there is little competition for light or space.

Scutellaria antirrhinoides is polymorphic for gland-tipped trichomes on vegetative and floral parts, but the presence of this character is not associated with any other morphological distinction or with geographic distribution. This species also is variable for flower size, with longer-flowered plants (20–23 mm) found in Humboldt, Del Norte, and Siskiyou counties in California and in southwestern Oregon (noted as "coastal form" on many collections by Tracy from the coastal forest of northern California). In areas where *S. siphocampyloides* occurs in close proximity to *S. antirrhinoides* (e.g., Lake, Trinity, and Shasta counties), flower size remains small (12–17 mm). This may represent a case of character displacement, if competition for pollinators occurs between these two species, whose flowers are similar in shape and color and differ primarily in size.

Hybridization has been observed between *S. antirrhinoides* and *S. californica*; see discussion under *S. californica*.

Scutellaria antirrhinoides previously has been circumscribed more broadly to include plants from northern California, western Oregon, southeastern Oregon, northern Nevada, and southwestern Idaho in one morphologically variable taxon. Experimental evidence from allozyme analysis shows a clear-cut distinction between a western taxon, *S. antirrhinoides* (northern California and western Oregon), and an eastern taxon, *S. angustifolia* subsp. *micrantha* (southeast Oregon and adjacent Idaho and Nevada). *Scutellaria antirrhinoides* is phylogenetically closest to *S. californica* and *S. siphocampyloides*, both of California, while *S. angustifolia* subsp. *micrantha* is phylogenetically closest to *S. angustifolia* subsp. *angustifolia* (Olmstead 1989).

The type of *S. antirrhinoides* was collected by Scouler near "Fort Vancouver," located at the present site of Vancouver, Washington, on the Columbia River. No subsequent collections of *Scutellaria* referable to this complex have been made from this vicinity. The nearest other collections with explicit locality information represent two taxa, *S. angustifolia* subsp. *angustifolia* collected on the Washington side of the Columbia River, ca. 50 mi east of Vancouver (Olmstead 561, Suksdorf 6577), and *S. antirrhinoides* collected in the lower Willamette Valley, ca 30 miles south of Vancouver (Lloyd s.n., Sheldon 12236). Of these two taxa, the type specimen clearly represents *S. antirrhinoides*. It is difficult to be certain on the basis of morphology alone that the type of *S. antirrhinoides* does not represent *S. angustifolia* subsp. *micrantha*. However, the distribution of *S. angustifolia* subsp. *micrantha* is entirely east of the Cascades with the nearest known locality in southeastern Oregon, whereas populations attributable to *S. antirrhinoides* are distributed continuously from northern California through Oregon west of the Cascades to locations very close to the type locality. One population from the west slope of the Cascades near Eugene (Olmstead 922) has been determined allozymically to belong to *S. antirrhinoides* (Olmstead, unpub.).

REPRESENTATIVE SPECIMENS: CALIFORNIA. Colusa Co.: Snow Mt, SE side above Bonnie View, Heller 13234 (CAS, DS, GH, MO, NY, PH, US, WTU). Del Norte Co.: N bank cliffs, Klamath trail, Van

Deventer 247 (JEPS); Smith River, *Parks* 24020 (DS, GH, MICH, MO, NY, PH, RM, UC, US, WTU); near Gasquet, *Eastwood & Howell* 3766 (CAS); 35 mi up the Smith River from Crescent City, *Thompson* 4560 (DS, MO, WTU). Glenn Co.: Plaskett Meadows, *Howell* 19829 (CAS, WTU); summit ridge N of Black Butte, *Howell* 19027 (CAS, NY). Humboldt Co.: Carlotta, *Tracy* 13238 (UC); Brannan Mt, *Tracy* 12654 (UC); Grouse Mt, serpentine area on Friday Ridge near Clear Lake, *Tracy* 19231 (WTU); 5 mi N of Garberville, *Tracy* 17167 (WTU); Twin Lakes vicinity, *Tracy* 19577 (UC, WTU); Avenue of the Giants, 0.9 mi S of Miranda, *Olmstead* 421, 780 (WTU); 2 mi N of Alderpoint on road to Blocksburg, *Olmstead* 424 (WTU); Hupa Indian Reservation, *Chandler* 1323 (MO, NY, TEX, UC, US); near Blocksburg, 2 mi S of town, *Tracy* 15875 (LA, UC, WTU); near Beebe's ranch, 3 mi NW of jct of Willow Cr with Trinity River, *Tracy* 3399 (DS, GH, MO, RM, UC, US). Lake Co.: Snow Mt, Crooked tree ridge, 2 mi NW of summit, *Olmstead* 878 (WTU); slopes above Summit Lake, Mt Sanhedrin, *Hall* 9477 (NY, UC, US); Snow Mt, Crooked Tree Ridge, NW side of Mt, *Heckard & Hickman* 5962 (JEPS). Lassen Co.: Big Valley Mtns, *Eastwood & Howell* 7978 (CAS). Mendocino Co.: Sherwood Valley, *Jepson* 1829 (JEPS). Modoc Co.: margin of Egg Lake, *Baker s.n.* (UC); on lava side, near rocky shore, *Baker s.n.* (DS, NY, UC). Plumas Co.: 7 mi SW of Westwood, near Lake Almanore, *Grinnell s.n.* (JEPS); Prattville, *Heller & Kennedy* 8798 (CAS, DS, GH, MO, NY, PH, US); near mouth of Little Grizzly Cr below Genesee, *Heller & Kennedy* 8843 (CAS, GH, MO, NY, PH, US). Shasta Co.: Squaw Cr Ranger Station, *Drew s.n.* (DS, NY, US); Pitt River, *Smith* 316 (CAS, GH, US); Wallace Ranch, Goose Valley, *Peirson* 10327 (UC); Little Hatchet Cr, W side of Hatchet Mt. 3 mi W of summit, W of Burney, *Quick* 66-30 (CAS); near Fall Creek Inn, along Gilman Rd, between the Sacramento and McCloud arms of Shasta Lake, *Heckard et al.* 2314 (JEPS); Goose Valley, *Eastwood* 793 (CAS, GH, MO, NY, US). Siskiyou Co.: S fork Salmon River between campground and Carter's, *Ferlatte* 266 (JEPS); N Fork Salmon River, 6 mi W of Sawyer's Bar, 1 mi E of Red Bank campground, *Olmstead* 472 (UC, WTU); Big Flat Campground, S Fork Salmon River, *Olmstead* 465 (WTU); Klamathon, *Copeland* 3530 (GH, MICH, MO, TEX, NY, UC); Marble Mtns Wilderness Area, vicinity of English Peak, below English Lake, *Oettinger* 1128 (MICH, UC); Compton's Prairie, N base of Mt. Eddy, *Heller* 13270 (CAS, DS, GH, MO, PH, UC, US, WTU); Metcalf's ranch, NE base of Mt Eddy, *Heller* 12111 (CAS, DS, GH, MO, NY, PH, US, WTU). Sonoma Co.: S slopes of Fitch Mt, near Healdsburg, *Rubtzoff* 1163 (CAS). Tehama Co.: S Yolla Bolly Mt, E of Mt Linn summit, *Bacigalupi et al.* 5321 (JEPS); S Yolla Bolly Mt, 0.5 mi E of Ides Cove on SE side of mt, *Tucker* 3566 (CAS, DS, UC). Trinity Co.: Trinity River above confluence with Ramshorn Cr, *Bacigalupi et al.* 3737 (JEPS); on serpentine, N side of Red Lassic Peak, *Hoffman* 2890 (UC); hillside SW of S Dukabella Mt, *Smith & Sawyer* 6996 (WTU); Swift Creek, just above Trinity Center, *Voss* 13003 (WTU); Van Duzen River, 9.5 mi above Hwy 34 jct on Forest Hwy 511 and 1S07, *Olmstead* 429, 886 (RENO, UC, US, WTU); along Hwy 36, 0.5 mi W of Six Rivers N.F. and Trinity N.F. boundary, *Olmstead* 437 (CAS, WTU); Canyon Cr Trail, 1.5 mi from trailhead, N of Dedrick, *Olmstead* 452 (UC, WTU); Coffee Cr Rd, 1 mi above confluence with Union Cr, *Olmstead* 461 (NY, OSC, WIS, WTU); Hwy 3 near Scott Mt Cr, S of Scott Mt pass, *Olmstead* 467 (CAS, WTU); Nash mine, Coffee Cr at mouth of Union Cr, *Hall* 8556 (GH, NY, UC, US); 1.5 mi N of trailhead on Canyon Cr trail, 5.5 mi N of Dedrick, *Denton* 4305 (WTU). Locale uncertain: Cahto, *Kellogg & Harford* 741 (CAS, GH, MO, NY, PH).—OREGON. Benton Co.: one mi N of Corvallis, *Wall & Owens s.n.* (WTU). Clackamas Co.: Willamette Falls, *Sheldon* 12236 (DS). Curry Co.: Rogue River canyon, 1.5 mi S of Illahe, *Baker* 6096 (NY, OSC, UC, WTU); banks of Illinois River above Oak Flat, 5 mi S of Agness, *Baker* 5507 (OSC, WTU). Douglas Co.: Nickel Mt, *Detling* 6332 (DS, UC, WTU). Jackson Co.: Howard Prairie Dam, *Dennis* 2263 (CAS, DS, OSC, NY); mountain meadow 20 mi S of Prospect, *Thompson* 13089 (LA, NY, PH, WTU); 1.9 mi W of Rogue River, along River Rd, *Olmstead* 656 (WTU); 7 mi SW of Prospect, *Hitchcock & Martin* 4998 (NY, WTU); summit of Cascade Mtns near Pinehurst, *Thompson* 13145 (CAS, GH, MO, NY, PH, US, WTU); Golden Stair Trail, E fork of Abbott Cr, 20 mi W of Crater Lake, *Mitchell* 107 (OSC, RM). Josephine Co.: Rogue River Trail, 0.5 mi below confluence with Grave Cr, *Olmstead* 654 (WTU); 10 mi S of Kerby, *Thompson* 4613 (DS, MO, OSC, PH); Grant's Pass, *Howell s.n.* (GH, NY, TEX, US, WTU). Klamath Co.: near head of Denny Cr, W of Klamath Lake, *Applegate* 3710 (DS, LA, UC, OSC); Hayden Mt, *Jepson* 18461 (JEPS); Long Lake on E side, *Applegate* 3713 (GH, UC, OSC); woods near Rock Cr bridge, W side of Upper Klamath Lake, *Peak* 9463 (DS, GH, MO, NY, OSC, PH). Lane Co.: 10 mi NW of Oakridge, *Peck* 22092 (UC); Sharp's Cr, Dorena, E of Cottage Grove, *Constance s.n.* (UC); Fall Creek, *Bradshaw* 2060 (DS). Marion Co.: 2 mi E of Stayton, *Nelson* 4072 (PH). Washington Co.: Forest Grove, *Lloyd s.n.* (NY).

Scutellaria bolanderi Gray, Proc. Amer. Acad. Arts 7: 387. 1868.—TYPE: USA. California: Mariposa Co., Clark's Meadow, Wawona, Yosemite National Park, 1866, *Bolander* 5006 (holotype: GH!; isotypes: LA! UC! US!).

Plants (20–) 30–80 (–100) cm tall, perennating by slender rhizomes swollen at the ends; stems single or branched near the base, erect or decumbent; stems and leaves moderately to densely covered with spreading trichomes 1.0–2.0 mm long and frequently covered with gland-tipped trichomes. Basal leaves with petioles 2–10 mm long; leaves below first flowering node short-petiolate to sessile, the blades ovate to cordate, crenate, the apices rounded; leaves above first flowering node sessile, the blades ovate to cordate, with margins crenate or rarely entire, the apices rounded; leaf at first flowering node 20–40 mm long, 10–25 mm wide, mean length/width = 1.8. Flowers axillary, first appearing 10–15 nodes above base of stem and continuing up the stem; pedicels 2.0–3.0 mm long; calyx 3.0–5.0 mm long, the upper lobe with concave transverse crest scalloped on the apex; corolla white mottled with blue on the lower lip, 13–19 mm long, personate, pubescent with gland-tipped trichomes abaxially, pilose with long, tangled hairs adaxially, the palate covered with scattered, long trichomes; filaments attached near or above the middle of the corolla tube; gynoecial disk green-yellow. Nutlets brown to black, ovoid to subglobose, 1.1–1.3 mm long, 1.0–1.3 mm wide, covered with small cylindrical papillae, surrounded by a distinct circumferential band, sparsely covered with sessile glands. Chromosome number: $2n=24$. Figs. 1c, 2c,d, 5i–l.

Scutellaria bolanderi resembles the widespread *S. galericulata* in habit, leaf shape (cordate base and crenate/dentate margins), and wet-site habitat. Experimental evidence from isozyme analysis indicates that *S. bolanderi* is as similar to *S. galericulata* (represented in the analysis by a single population from the western U.S.) as it is to other species of the *S. angustifolia* complex (Olmstead 1989). However, differences in chromosome number, nutlet morphology, floral morphology, and flowering phenology between *S. bolanderi* and *S. galericulata* indicate that *S. bolanderi* has a closer phylogenetic relationship to the *S. angustifolia* complex than to *S. galericulata*. The morphological and isozymic similarities apparently represent shared ancestral characters between the two taxa (Olmstead 1989).

Scutellaria bolanderi consists of two subspecies. Restricted to wet gravel in the margins of small streams, it is one of the most ecologically distinctive members of the group. Subspecies *bolanderi* occurs in the Sierra Nevada foothills and subsp. *austromontana* in the mountains of southern California. Subspecies *austromontana* is distinguished from subsp. *bolanderi* by a shorter corolla (13 mm vs. 17 mm) and a broader leaf outline (leaf l/w = 2.1 vs. 1.7). The morphological distinctions between these two subspecies and their geographic isolation is reflected in the relatively low genetic similarity between them (Olmstead 1989); Nei's genetic identity (Nei 1978) equals 0.88.

***Scutellaria bolanderi* subsp. *bolanderi*.**

Leaf length less than two times the width (mean length/width = 1.7); upper leaves always crenate; corolla 15–19 mm long. Fig. 5i–l.

Phenology. Flowering June–August.

Distribution (Fig. 8). California in the foothills of the Sierra Nevada from Amador County to Kern County with an outlying distribution in the inner South Coast ranges in Santa Clara County; moist gravel along stream margins in valley oak woodland and digger pine woodland; 300–1500 m.

REPRESENTATIVE SPECIMENS: CALIFORNIA. Amador Co.: Jackson, W side of town in bed of Cr at Hwy 108 bridge, *Olmstead 401* (WTU); South Jackson, *Hansen 448* (UC). Calaveras Co.: margin of

O'Neil Cr, 1 mi N of Sheep Ranch, *Olmstead* 395 (WTU); small seep along Hwy 4, 2 mi W of Vallecitos, *Olmstead* 390 (UC, WTU); Coyote Cr, near bridge in Vallecitos on Parnott's Ferry rd, *Olmstead* 389 (UC, WTU); Waterman Cr, 3.5 mi W of Altaville on Hwy 4, *Bacigalupi et al.* 6371 (JEPS); Mokelumne Hill Ditch, Rattan's ranch, *Rattan s.n.* (UC); below Angel's Camp, near river, *Davy* 1486 (UC). Fresno Co.: 2 mi W of Clovis on rd to Cameo, *Nobs & Smith* 986 (UC); Rogers Valley, 4 mi N of Auberry, *Jepson* 12855 (JEPS); Tollhouse along Dry Cr, *Olmstead* 569 (CAS, US, WTU); in small creek along Watts Valley rd, 6.8 mi S of jct with Tollhouse rd, ca 9 mi S of Tollhouse, *Olmstead* 570 (NY, OSC, UC, WTU); Tollhouse, *Hall & Chandler* 39a (MO, NY, UC, US); Hitching Post Ranch, *Follansbee* 864 (TEX); Sierra National Forest, *Bentley & Magee* B-291 (RM); Sequoia Mills, *Eastwood s.n.* (GH). Kern Co.: Cedar Cr, below mouth of Fulton Cr, near Glennville, *Twisselman* 7706, 8507 (CAS); W side of Lynns Valley, *Twisselman* 11388 (CAS); Linns Valley, E side rd at small creek crossing 3.6 mi N of Glennville, *Olmstead* 821 (WTU); Poso Cr near Poso mine, *Smith* 2 (WTU); Howling Gulch, 2–3 mi SE of Woody, *Smith* 564 (JEPS); Lumreau Cr, just above Cedar Cr, near Glennville, *Twisselman* 11645 (CAS); Lynns Valley at the Henry Bowen ranch, *Twisselman* 9961 (CAS). Madera Co.: Sagamore Cr, 1.5 mi W of bridge on rd from Italian Bar bridge to North Fork, *Quibell & Quibell* 2453 (UC); stream next to Hwy 41 ca 2 mi N of Coarsegold, *Olmstead* 836 (WTU); Gold Cr at crossing 4 mi S of Bass L and 3 mi W of North Fork, *Olmstead* 379 (WTU); Whiskey Cr, *Bullard* 179 (UC); Coarsegold, *Epling s.n.* (LA); San Jaquin Experimental Range Station, *Biswell* B-96 (RM). Mariposa Co.: Wawona (Clark's) Meadow, Yosemite Nat Park, *Haines & Haines s.n.* (LA, WIS); Agua Fria Rd, ca 1 mi S of Mt Bullion, *Olmstead* 374 (CAS, NY, WTU); Wawona, *Hall* 9002 (UC); Mariposa, *Congdon s.n.* (NY, UC); Clark's Meadow, Yosemite Nat Park, *McClellan s.n.* (UC); Mariposa, *Congdon s.n.* (MO); Wawona, *Epling s.n.* (LA); Mariposa Co., *Hollick s.n.* (NY); Chowchilla rd near Cold Springs ranch, *Tilforth* 678 (OSC). Santa Clara Co.: Bradleys Store on Uvas Cr, *Epling & Simmons s.n.* (LA). Tulare Co.: Grant Forest, *Brandegee s.n.* (UC); Kaweah River basin, *Hopping* 33 (UC); Three Rivers, *Culbertson* 4199 (GH, MICH, MO, NY, UC); Eshom Valley, *Clemens s.n.* (RM). Tuolumne Co.: Sittle Flat Gulch above Indian Cr, *Williamson* 167 (RM, UC); creek along Wards Ferry rd, 2 mi NE of Groveland, *Olmstead* 386 (WIS, WTU); Standard City, *Hoover* 2552 (UC); base of reservoir dam, Twain Harte, *Etienne s.n.* (CAS); vicinity of Rawhide, John Gillam Gulch, *Stinchfield* 44 (MICH, NY).

Scutellaria bolanderi subsp. **austromontana** Epling, Madroño 5: 58. 1939.—TYPE: USA. California. San Diego Co., along Carrizo Creek, near Lake Henshaw, 10 Jul 1936, *Gander* 2739 (holotype: LA!; isotype: SD!).

Leaf length at least two times the width (mean length/width = 2.1); upper leaves crenate or rarely entire; corollas 12–14 mm long. Figs. 1c, 2c,d.

Phenology. Flowering June–August.

Distribution (Fig. 8). Mountains of southern California from San Bernardino County to San Diego County; moist gravel along stream margins in valley oak and yellow pine woodlands; 600–2000 m.

REPRESENTATIVE SPECIMENS: CALIFORNIA. Riverside Co.: Keenwild Ranger Station, 0.4 mi N of Mountain Center, ca 3.5 mi S of Idylwild, along Hwy 243, *Olmstead* 803 (WTU); junction of Palms to Pines Hwy and Idylwild Rd, *Epling s.n.* (LA, WTU); San Jacinto Mts, along San Jacinto River, *Hall* 696 (MO, UC, US); San Jacinto Mts, *Hall s.n.* (NY); Idylwild, *Spencer* 2333 (GH); San Jacinto Mts, *Parish* 474 (GH, MO, NY, PH, US). San Bernardino Co.: meadows, Victorville, *Parrish* 10599 (RM, UC); banks of the Mojave River, *Parrish s.n.* (UC). San Diego Co.: Palomar, Smiths Mt, *McClatchie s.n.* (NY, UC); Cuyamaca, *Brandegee s.n.* (UC); junction of Warner Hot Springs and Lake Henshaw rd, *Epling s.n.* (LA); Boulder Cr below Cuyamaca Dam, *Wiggins* 2694 (DS); Deer Park, Cuyamaca Mts, *Chandler* 5468 (NY, UC); Palomar, *Brandegee s.n.* (UC); Julian, near San Diego, *Orcutt s.n.* (MO); Smith Mt, near San Diego, *Orcutt* 429 (MO, US); Fry Cr, at campground, S of Palomar observatory, *Tilfourth & Dourly* 453 (GH).

Scutellaria brittonii Porter, Bull. Torrey Bot. Club 21: 177. 1894.—TYPE: USA. Colorado: Clear Creek Cañon, 9000 ft, 15 Jun 1875, *Coulter s.n.* (holotype: PH!; isotypes: NY! PH! US!).

Scutellaria virgulata Nelson, Bull. Torrey Bot. Club 25: 283. 1898. *Scutellaria brittonii* var. *virgulata* (Nelson) Rydberg, Fl. Colorado 296. 1906.—TYPE:

USA. Wyoming: Laramie Hills, Green Top, 9000 ft, 28 Jun 1897, *Nelson* 3218 (holotype: RM!; isotypes: GH! MO! NY! US!).

Plants 10–20 (–30) cm tall, perennating by slender rhizomes swollen at the ends; stems single or branched near the base; stems and leaves moderately covered with trichomes 0.05–0.2 mm long and appressed-descending, and occasionally sparsely to densely covered with gland-tipped trichomes. Basal leaves with petioles 2–5 mm long; leaves below first flowering node short-petiolate to sessile, the blades ovate, entire, the apices rounded to acute; leaves above first flowering node sessile, the blades ovate to oblong, entire, the apices rounded to acute; leaf at first flowering node 20–30 mm long, 5–10 mm wide, mean length/width = 3.3. Flowers axillary, first appearing 5–8 nodes above base of stem and continuing up the stem; pedicels 3.0–4.0 mm long; calyx 4.5–5.5 mm long, with concave transverse crest on upper lobe; corolla violet-blue, 25–30 mm long, personate, pubescent with gland-tipped trichomes abaxially, glabrous adaxially, the lower lip with white patch mottled with violet; filaments attached above the middle of the corolla tube; gynoeceal disk green-yellow. Nutlets black, ovoid, 1.8–2.0 mm long, 1.5–1.6 mm wide, covered with large conical papillae, with or without a circumferential band, sparsely covered with sessile glands. Chromosome number: $2n=22$. Figs. 4e,f, 5m–p.

Phenology. Flowering May–July.

Distribution (Fig. 9). Southeastern Wyoming and adjacent southwestern Ne-

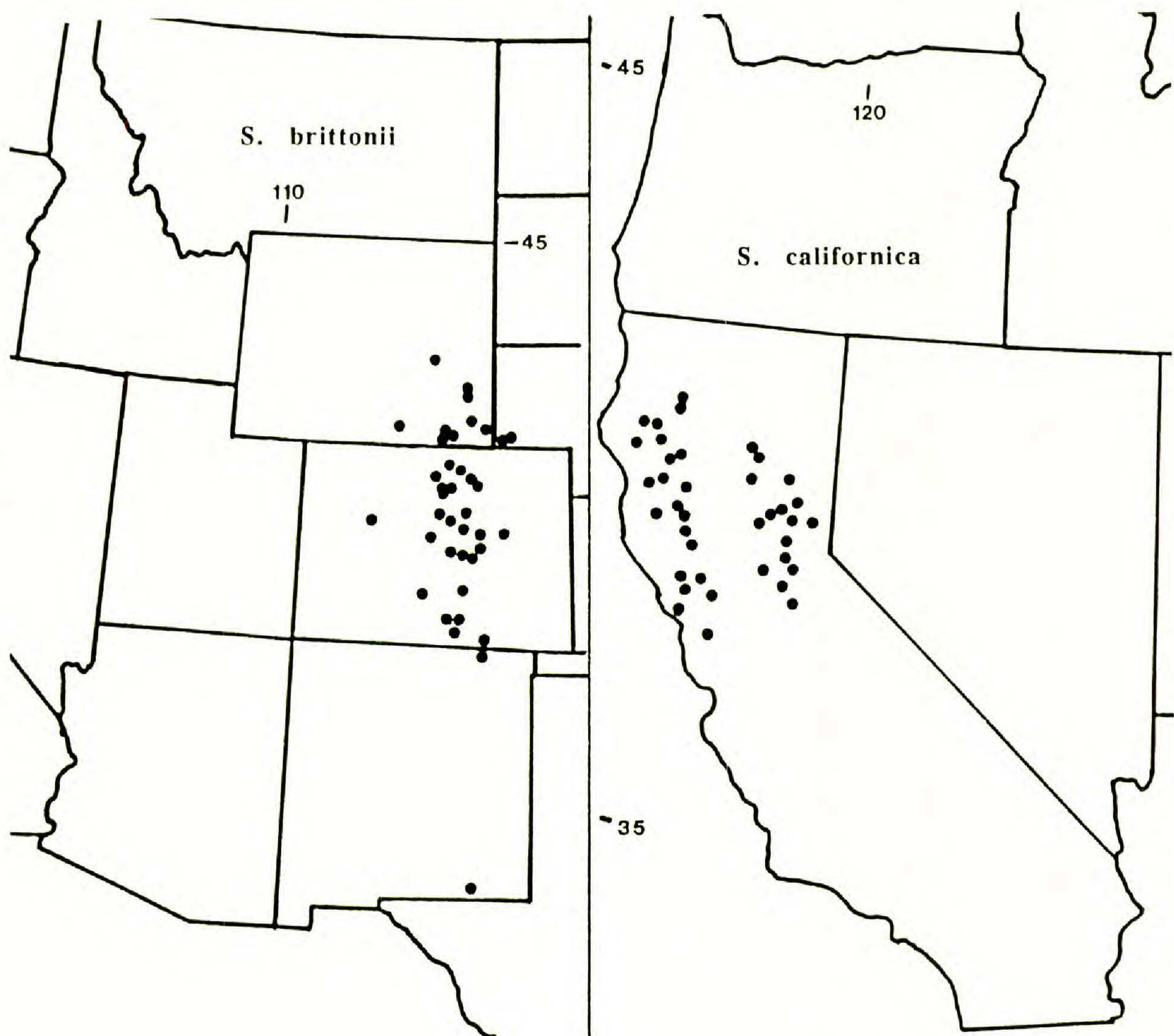


FIG. 9. Distribution of *Scutellaria brittonii* and *S. californica*.

braska south through Colorado to northeastern New Mexico along the front range of the Rockies, with outlying collections reported from Glenwood Springs in western Colorado, and Carlsbad Caverns in southern New Mexico; coarse granitic soil in ponderosa pine woodland; 1600–3300 m.

Scutellaria brittonii represents a geographic outlier from the rest of the complex, occurring in the front range of the Rockies. It is unique in the group for its chromosome number, $2n=22$ (all other taxa have $2n=24$). In corolla morphology, *S. brittonii* is similar in size and shape to *S. angustifolia* subsp. *angustifolia* and *S. siphocampyloides*, but can be distinguished morphologically from them by the presence of down-curved hairs on the stem, leaves with prominent main veins abaxially and rounded to acute leaf apices, and nutlets with large conical papillae. *Scutellaria brittonii* is polymorphic for the presence of gland-tipped hairs on the stems, leaves, and flowers.

The identity of this taxon remained a source of confusion for many years following its discovery as a result of a case of mistaken identity by Asa Gray. In the *Synoptical Flora of North America*, Gray (1878) included descriptive and distributional information with the name *S. resinosa* Torrey that described *S. brittonii* rather than the *S. resinosa* described by Torrey (1828). Sixteen years later, Porter (1894) recognized this error and rectified it by assigning the name *S. brittonii* to the Rocky Mt specimens matching the description in Gray (1878).

REPRESENTATIVE SPECIMENS: NEBRASKA. Kimball Co.: 2 mi W of Kimball, *Stephens 11664* (DS, GH, NY); 2 mi E of Pine Bluffs, WY, and 1.5 mi S, *Churchill 7376* (MO, NY); 0.6 mi W of Kimball, *Lane & Stull 403* (NY).—WYOMING. Albany Co.: Green Top, Laramie Hills, *Nelson 3147* (MICH, RM, UC); vicinity of Vedawoo Glen, Laramie Mts, *Rollins 992* (DS, GH, US); Laramie range, Pole Mt District, Medicine Bow National Forest, W of Eagle Rock, *Aslamy 147* (RM); Laramie range, foothills near Telephone Canyon, *Porter 6967* (DS); Laramie Hills, *Nelson 1918* (GH, RM, US, WIS); Sand Cr, *Nelson 7009* (GH, MO, NY, RM, US); mouth of Telephone Canyon, *Williams 2225* (GH, MO, US); sandy prairie E of Laramie, *Porter 3199* (MO, NY, WTU); Wheatland cut-off, Sybille canyon, ca 3 mi NE of Morton Pass, *Hartman 2975* (RM). Carbon Co.: along N Platte River in N Gate Canyon at Six Mile Gap, *B. Nelson 520* (RM). Converse Co.: Box Canyon, upper Wagon Hound Cr, *Rollins 26* (MO). Laramie Co.: along Hwy 87, 20–30 mi N of Cheyenne, *Porter & Porter 8673* (GH, RM, WTU); 9.5 mi NE of Cheyenne on Chalk Bluffs rd, *B. Nelson & Ehrmann 1716* (NY, RM); 3.3 mi N of Burns on Hwy 214, *Lane & Stull 398* (NY). Platte Co.: Little Cottonwood draw, 10 mi NE of Wheatland on county rd, *B. Nelson 1485* (NY, RM); 3.5 mi W of Guernsey, *Wherry s.n.* (PH). Locale uncertain: Pole Cr. near Table Mt, *Nelson 94* (GH, MO, NY, PH, RM, US).—COLORADO. Arapaho Co.: 5 mi SW of Kenwood, *Pohl 1932* (PH). Boulder Co.: 4 mi N of Ward along Hwy 72, *Olmstead 642* (WTU); 2 mi S of Boulder, *Ramaley 15984* (MO, PH, RM, TEX, US); St. Vrain Canyon, *Coulter s.n.* (NY); foothills near Boulder, *Tweedy 5571* (NY, RM); foothills near Boulder, *Patterson 296* (GH, MICH, MO, NY, PH, US); Gregory Canyon near Boulder, *Hansen C211* (MO); Eldora, *Payson s.n.* (MO, RM). Clear Creek Co.: Brookvale, *Churchill s.n.* (GH, MO, US); Arapaho Nat. Forest, *Gierisch 1241* (NY, RM, WIS). Costilla Co.: Veta Pass, *Rydberg & Vreeland 5668* (NY, RM). Douglas Co.: 15 mi S of Castle Rock, *Snyder & Beetle 75* (MO, NY, PH, RM); 4 mi E of Franktown, *Lane & Stull 391* (NY). Elbert Co.: 15 mi SW of Limon on Hwy 24, *Cox et al. 166* (MO); Kiowa Cr between Kiowa and Elbert, *Ewan 12859* (NY). El Paso Co.: eastern base of Cheyenne Mt, near Colorado Springs, *Rollins 1201* (MO, NY); Manitou, just above the cog station at foot of N slope of Pikes Peak, *Johnston 2630* (MO, UC); Colorado Springs, *M. E. Jones s.n.* (NY, RM, US); near Eastonville, *Eggleston 11181* (US); 3.9 mi N of Peyton on Bradshaw rd, *Lane & Stull 390* (NY); Ute Pass, Colorado Springs, *M. E. Jones 83* (NY, US); Cañon City, *Brandegge B413* (MO, PH, RM). Garfield Co.: Glenwood Springs, *Osterhout 2587* (NY, PH, RM); Grizzly Cr, Hwy 24, 6 mi E of Glenwood Springs, *Pennell & Schaeffer 22185* (PH). Gilpin Co.: Eldora to Baltimore, *Tweedy 5570* (NY, RM). Huerfano Co.: Cuchara River below Le Veta, *Rydberg & Vreeland 5671* (NY, RM); Cucharas Pass, *Nelson & Nelson 4710* (DS, RM). Jefferson Co.: Apex Canyon, *Clokey 3060* (MO, RM, TEX, US). Larimer Co.: E of Fort Collins, *Crandall 1707* (NY, US); Greyrock Mt trail, 10.5 WNW of Laporte, *Hermann 23640* (RM); Poudre Canyon, 3 mi W of Hwy 287 on Hwy 14, *Nelson & Nelson 1204* (NY, RM); Bear Lake rd, Rocky Mt Nat Park, *Whitehouse 18818* (NY, US). Las Animas

Co.: Raton Pass, 14 mi S of Trinidad, *Williams* 2274 (MO, UC); near Trinidad, 2 mi N of Pergatoire River, *Rollins* 1802 (GH, MO, NY). Park Co.: 2 mi S of Hwy 285 at Pine Jct, *Shea & Shea* 59 (MO). Pueblo Co.: near Beulah, *Robbins* 4886 (RM). Saguache Co.: Saguache, *Lockett* 23235 (WIS). Teller Co.: Florissant, *Cockerell s.n.* (NY, RM). Weld Co.: bluffs SE of Windsor, *Osterhout* 6174 (RM); Evans, *Johnston* 162A (MO); T10N, R66W, S2, *Snyder S-89* (RM) Locale uncertain: 'Cross Ruxton, *Clements* 95 (GH, MO, NY, RM, US); Murley, E of town, *Johnston & Hedgcock* 870 (GH, RM); Rocky Mts, *Hall & Harbour* 431 (GH, MO, NY, PH, US).—NEW MEXICO. Colfax Co.: Raton Pass, *McKelvey* 4869 (NY, PH); near summit of Raton Pass, N of Raton, *Matthias* 517 (MO). Eddy Co.: Carlsbad Caverns, *Nelson* 11372 (GH, MO, NY, PH, RM, UC). Locale uncertain: near Turkey Mt, *Harris* 21 (US).

Scutellaria californica Gray, Syn. Fl. 2: 381. 1878. *Scutellaria antirrhinoides* var. *californica* Gray, Proc. Amer. Acad. 8: 396. 1873. *Scutellaria bolanderi* var. *californica* (Gray) Penland, Rhodora 26: 68. 1924.—TYPE: USA. California: Anderson Valley, Mendocino Co., 1866, *Bolander* 4833 (lectotype designated by Epling, 1942: GH!; isoelectotypes: UC! US!).

Plants (15–) 20–35 (–40) cm tall, perennating by slender rhizomes swollen at the ends or occasionally by persistent root crowns; stems single or branched near base; stems and leaves moderately covered with trichomes 0.1–0.2 mm long and appressed ascending, sparsely covered with gland-tipped trichomes (occasionally lacking). Basal leaves often turning red and then deciduous, with petioles 5–10 mm long; leaves below first flowering node short-petiolate to sessile, the blades ovate, crenate, the apices rounded; leaves above first flowering node sessile, the blades ovate to oblong, entire, the apices rounded; leaf at first flowering node 15–25 (–35) mm long, 5–9 mm wide, mean length/width = 2.9. Flowers axillary, first appearing 8–11 nodes above base of stem and continuing up the stem; pedicels 3.5–4.5 mm long; calyx 3.5–5.0 mm long, with concave transverse crest on upper lobe; corolla white to cream-colored, occasionally tinged with pink or blue, 16–19 mm long, personate, covered with gland-tipped trichomes abaxially, with long, tangled hairs on palate and lower side of tube adaxially; filaments pilose, attached below the middle of the corolla tube; gynoeceal disk green-yellow. Nutlets black, ovoid, 1.6–1.8 mm long, 1.3–1.5 mm wide, covered with small cylindrical papillae or nearly smooth, surrounded by an indistinct circumferential band, with scattered sessile glands. Chromosome number: $2n=24$. Figs. 3c–e, 10a–d.

Phenology. Flowering May through July.

Distribution (Fig. 9). California, the North Coast Ranges from the San Francisco Bay area north to Humboldt and Trinity Counties and the northern Sierra Nevada foothills from Calaveras County to Butte and Plumas Counties; openings in mixed conifer forest, yellow pine woodland, digger pine woodland, oak woodland, and oak-shrub communities; 300–2000 m.

Scutellaria californica is the only species in the *S. angustifolia* complex that will occasionally produce shoots from the same root crown for consecutive growing seasons as evidenced by the frequent occurrence of dead stems of the past year with flowering stems of the current year. *Scutellaria californica* is a morphologically homogeneous species and is most similar in vegetative morphology to *S. antirrhinoides*, *S. angustifolia*, and *S. siphocampyloides*, but it can be distinguished readily from these blue-flowered taxa by its white corolla. The two other white-flowered taxa, *S. nana* and *S. bolanderi*, can be distinguished from *S. californica* by habit and by minor differences in corolla markings. *Scutellaria californica* has erect, usually unbranched stems and has corollas of uniform color without markings. In contrast to *S. californica*, *S. nana* has a dwarf habit (rarely greater than 10 cm in height) and a corolla

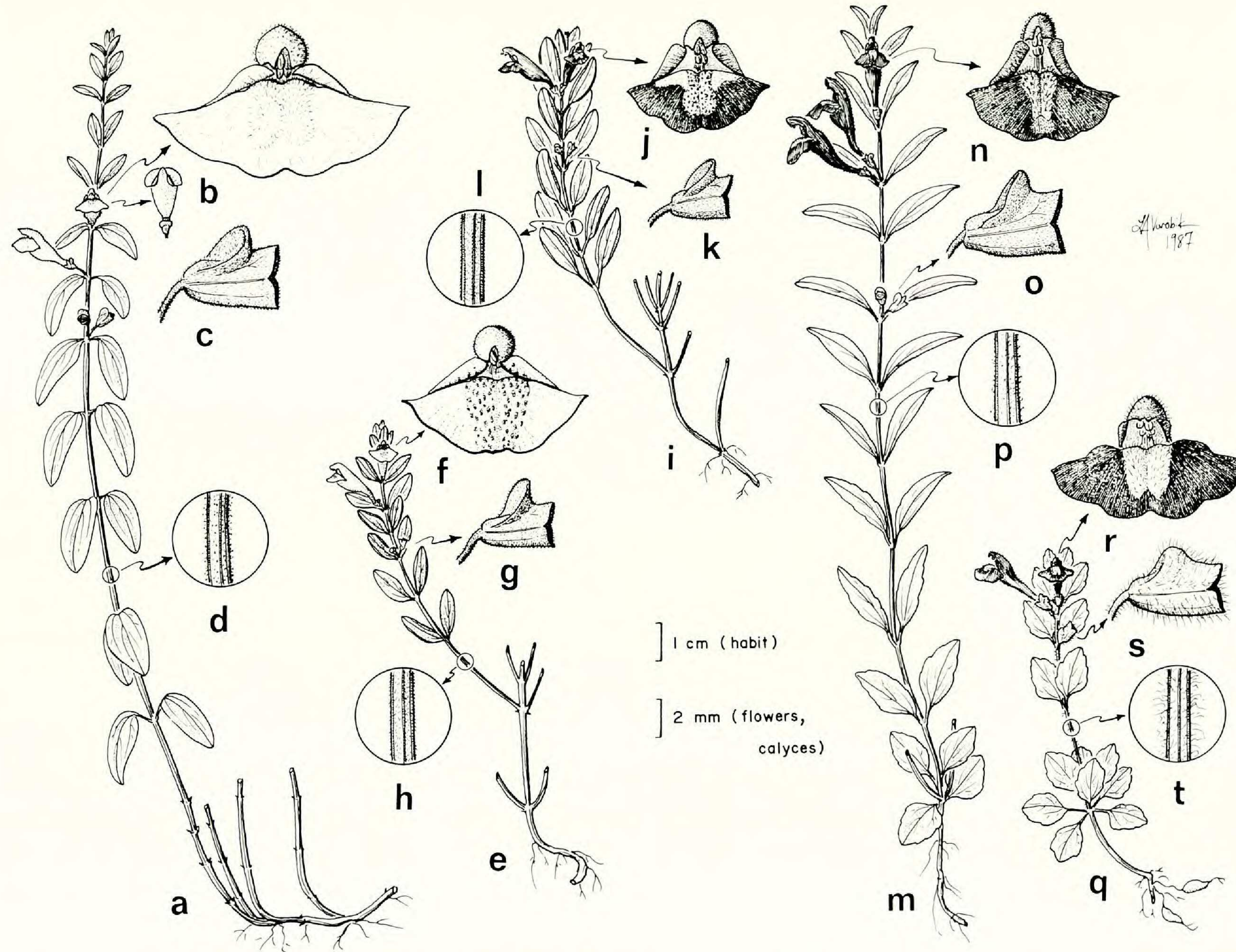


FIG. 10. *Scutellaria californica*, *S. nana*, *S. sapphirina*, *S. siphocampyloides*, and *S. tuberosa*. a–d. *S. californica* (from Olmstead 436). a. Habit. b. Corolla. c. Calyx. d. Section of stem with trichomes. e–h. *S. nana* (from Olmstead 415). e. Habit. f. Corolla. g. Calyx. h. Section of stem with trichomes. i–l. *S. sapphirina* (from Olmstead 596). i. Habit. j. Corolla. k. Calyx. l. Section of stem with trichomes. m–p. *S. siphocampyloides* (from Olmstead 677). m. Habit. n. Corolla. o. Calyx. p. Section of stem with trichomes. q–t. *S. tuberosa* (from Olmstead 535). q. Habit. r. Corolla. s. Calyx. t. Section of stem with trichomes.

with the upper lip commonly tinged with purple and the lower lip with purple markings. *Scutellaria bolanderi* has a tall (30–80 cm in height), coarse, often multi-branched habit and corollas with blue-spotted lower lips.

S. antirrhinoides has greater variation in corolla length than *S. californica*, but the average corolla length for both taxa is similar. In addition to corolla color there is a difference in shape of the corolla that distinguishes the two taxa: *S. antirrhinoides* has an attenuated, funnellform corolla outline when viewed from above, whereas *S. californica* has a cuneiform corolla outline when viewed from above and is more gibbous ventrally, resulting in a broader corolla outline when pressed (Figs. 5f, 10b). The shape difference is a result of greater elongation of the lower portion of the corolla tube in *S. antirrhinoides* than in *S. californica* and is evident from a comparison of the fusion of the filament and corolla tube: greater than half the length of the tube in *S. antirrhinoides* and less than half the length in *S. californica*.

Scutellaria californica is a morphologically homogeneous species with less variation in flower size, leaf shape, pubescence, and nutlet size than is typically observed in other species within the group. A form with unusual nutlet morphology, devoid of surface papillae, is distributed in the vicinity of Lake County (Fig. 3e). A considerable degree of isozymic differentiation exists between the Coast Range populations and the Sierra Nevada populations, with a mean genetic similarity of 0.86 for comparisons between populations across the disjunction compared to mean genetic similarities of 0.94 for populations in the Coast range and 0.92 for populations in the Sierra foothills (Olmstead 1988).

Hybrids between *S. californica* and *S. antirrhinoides* are known to exist in one location in Trinity Co. (Olmstead 887) and, on the basis of herbarium specimens and field observation, are believed to exist in other localities (Heckard & Hickman 1985; Denton, personal observation) where populations of the two species occur in close proximity (Colusa Co., Snow Mt., Heckard and Hickman 5772; Trinity Co., six miles above Ruth, Tracy 4314; Trinity Co., Hettenshaw Valley, Tracy 16959; Trinity Co., Canyon Cr. Lakes, Denton 4279). *Scutellaria californica* has been observed growing with *S. siphocampyloides* at one location in Lake Co. (Olmstead 671, 673), but without evidence of hybridization.

REPRESENTATIVE SPECIMENS: CALIFORNIA. Alameda Co.: Oakland hills, Torrey 405(a), 406 (GH, NY); Strawberry Canyon, Berkeley, Jepsen 9792, 9829 (JEPS). Amador Co.: Ione, Braunton 1917, 1047 (GH, MO, NY, UC, US); 1.2 mi NE of Amador City, Schreiber 2239 (UC). Butte Co.: Little Chico, Bruce 1825 (NY); Feather River Canyon, 25 mi NE of Oroville, Rose 40426 (LA). Calaveras Co.: Mokelumne Hill, Bigelow s.n. (GH, NY); San Antonio Cr, at road crossing between Sheep Ranch and Murphys, Chambers 4310 (OSC). Colusa Co.: 1.4 mi below Summit Springs, Snow Mt, Olmstead 881 (WTU); Snow Mt, E ridge of W peak, Heckard & Hickman 5772 (JEPS); Snow Mt, meadow in cirque area near Frog Pond, E of West peak, Heckard & Hickman 5450 (JEPS). El Dorado Co.: N of Sly Park, Hall 11382 (UC); 0.5 mi E of Whitehall resort along Hwy 50, Olmstead 402, 837 (UC, US, WTU); Simpson's ranch, Sweetwater Cr, Brandegee s.n. (LA, UC); N Fork Webber Cr, 3 mi E of Camino, Robbins 1241 (GH, UC). Glenn Co.: Plaskett Meadows, 8 mi SE of Mendocino Pass, Ownbey & Ownbey 1715 (GH, MICH, MO, NY, PH, RM, TEX, US); between Mud Flat and Bennett Spring on Newville-Covelo rd, Heller 11551a (GH, MO, NY, OSC, PH, US, UC). Humboldt Co.: S Fork of Eel River, 0.5 mi NW of S. Fork P.O., Constance 936 (JEPS); Buck Mt, lower foothills of NW slope, Tracy 15453 (GH, JEPS, LA, UC). Lake Co.: 0.5 mi W of Bear Cr. R.S., 20 mi N of Upper Lake, Olmstead 863 (WTU); 10.4 mi E of Bartlett Springs, near arm of Indian Valley Reservoir, Olmstead 666 (WTU); Bartlett Springs, roadside, Olmstead 371 (UC, WTU); open gravelly places near Hough's Springs, Heller 12379 (GH, NY, OSC, PH, UC, US, WTU); Elk Mt, northern Lake Co., Tracy 2297 (GH, UC, US, WTU); Bartlett Mt, Jepsen 18926 (JEPS); Lake County, Torrey s.n. (GH, NY, US). Marin Co.: Mt. Tamalpais, Eastwood 1530 (GH, MO, NY, US). Mendocino Co.: Hwy 20, Cold Cr, upper Russian River, Kappler 1726 (LA); 4 mi W of Covelo on road to Dos Rios, Oak Woodland, Hitchcock 20005

(WTU); 12.5 mi E of Hwy 101 on road to Covelo, *Wiggins 12136* (RM, UC, WTU); Orrs, *Eastwood 11388* (UC). Napa Co.: Tributary of Putah Cr, 5 mi S of Putah Creek, Napa, *Mason 8106* (UC); Napa Valley, *Greene 256?* (GH); Howell Mt, *Jepson 14933* (JEPS). Nevada Co.: 0.5 mi above Hwy 20, 1.5 mi N of Emigrant Gap, *Wiggins 11623* (RM, TEX, WTU); Donner Lake, *Hall & Babcock 4548* (MO, NY, RM, UC, US); 5 mi E of Emigrant Gap, *Keck 421* (UC); N shore of Bowman Lake, 1 mi E of junction of road to Hwy 20, *Heckard & Ornduff 2323* (JEPS); lower end of Donner Lake, *Heller 7020* (GH, MICH, MO, NY, PH, RM, UC, US, WTU). Placer Co.: Rattlesnake Cr, *Hall 8729* (UC); French Meadows, Middle Fork American River, *Smith 1670* (JEPS, RM). Plumas Co.: Quincy, *Clemens s.n.* (NY). Sacramento Co.: near Folsom, *Copeland 1630* (GH, UC). Sierra Co.: N Fork Yuba River, *Kappler 1340* (LA); along Hwy 49, 5.5 mi N of Camptonville, *Olmstead 844* (WTU); Hwy 49, 2 mi W of Sierra City, *Olmstead 409* (WTU); Hwy 49, 3 mi SW of Downieville, *Olmstead 407* (WTU). Solano Co.: Hillslopes, Suisun Valley, *Jepson 14932* (JEPS). Sonoma Co.: Petrified Forest, *Heller 5743* (GH, MO, NY, PH, RM, US); W of Cloverdale, *M. E. Jones 28823* (MO, UC); steep canyon hillslope, Sonoma Canyon, Kenwood, *Jepson 10002* (JEPS); Glen Ellen, *Brandegge s.n.* (UC). Tehama Co.: near Mineral, *Epling & Robison s.n.* (LA, MO, UC, US); Deer Cr, Hwy 32, 8 mi N of Butte Meadows, *Olmstead 416* (RENO, WTU); S base of S Yolla Bolly, *Munz 16959* (NY). Trinity Co.: Grasshopper Public Camp, 2.5 mi NW of Stuart Gap, N Yolla Bolly Mts, *Munz 16568* (NY, WTU); Trinity Mts, Canyon Cr, *Alexander & Kellogg 5436* (MICH, MO, RM, UC, WTU); Hettenshaw Valley, *Tracy 16959* (UC); 7.1 mi S of Hwy 34 on Forest Service rd 511, at bridge over Van Duzen River, *Olmstead 432, 887, 888* (CAS, US, WTU); E side of Hettenshaw Valley, *Olmstead 426* (CAS, NY, OSC, WTU); Canyon Cr trail, 2 mi N of trailhead, *Olmstead 453, 454* (CAS, WTU); Mad River at Hwy 36 bridge, *Olmstead 434* (NY, UC, WTU); Hwy 36, 2 mi SE of Mad River Camp, *Olmstead 435, 436* (UC, WTU); Canyon Cr at Ripstein Camp, *Olmstead 450* (UC, WTU); Salmon Trinity Alps Primitive Area, Canyon Cr Lakes, 10–12 mi N of Dedrick, *Denton 4279, 4280* (WTU); Ruth, gravelly flats along Mad River, *Tracy 8802* (UC, WTU); Canyon Cr trail, 6 mi N of Dedrick, *Hitchcock & Martin 5352* (LA, MO, NY, UC, US, WTU). Yuba Co.: Oregon Cr and Middle Fork Yuba River, 17 mi N of Nevada City on Hwy 49, *Olmstead 404, 839* (WIS, WTU); Hwy 49, 4 mi SW of Camptonville, *Balls & Lenz 21852* (OSC, RM, UC). Locale uncertain: *Bolander 6455=Rattan 255* (GH, UC, US); *Bridges 304, 304(a)* (GH, NY, US); *Hartweg 1918* (GH); *Kellogg & Harford 740, 743* (GH, MO, NY); *iiii Fremont s.n.* (GH, MO, NY, US).

Scutellaria nana Gray, Proc. Amer. Acad. 11: 100. 1876.—TYPE: USA. Nevada: Washoe Co., Winnemucca valley, near Pyramid Lake, 1874, *J. G. Lemmon s.n.* (holotype: GH!; isotype: UC!).

Scutellaria footeana Mulford, Bot. Gaz. 19: 118. 1894.—TYPE: USA. Idaho: Black Cañon, Boise River, 3500 ft, 18 Jun 1892, *Mulford s.n.* (holotype: GH!; isotypes: MO! NY!).

Scutellaria holmgreniorum Cronquist, Brittonia 33: 449. 1981.—TYPE: USA. California: Lassen Co., about 25 km SE of Ravendale, 5200 ft, 5 Jul 1980, *N. Holmgren & P. Holmgren 9524* (holotype: NY!; isotypes: NY! WTU!).

Plants 2–20 cm tall, perennating by thickened rhizomes; stems branched near the base; stems and leaves moderately covered with trichomes 0.1–0.2 mm long and appressed-descending, occasionally sparsely to densely covered with gland-tipped trichomes. Basal leaves with petioles 2–5 mm long; leaves below first flowering node short-petiolate to subsessile, the blades rhomboid to obovate, entire, and with rounded apices; leaves above first flowering node subsessile, the blades rhomboid, the apices rounded; leaf at first flowering node (10–) 15–20 (–25) mm long, 5–10 mm wide, mean length/width = 2.9. Flowers axillary, first appearing 3–7 nodes above base of stem and continuing up the stem; pedicels 1.0–3.0 mm long; calyx 3.0–4.0 mm long, with concave transverse crest on upper lobe; corolla creamy-white to ochroleucous, mottled with purple spots on lower lip, often tinted purple on upper lip, 15–20 mm long, personate, the abaxial surface pubescent and rarely covered with gland-tipped trichomes, the adaxial surface pilose with long, tangled hairs, the lower lip with scattered long trichomes or glabrous; filaments attached

above the middle of the corolla tube; gynoecial disk orange-red. Nutlets black, ovoid, 1.5–1.8 mm long, 1.3–1.5 mm wide, covered with small cylindrical to conical papillae, with or without a distinct circumferential band, sparsely covered with sessile glands or eglandular. Chromosome number: $2n=24$. Figs. 4a,b, 10e–h.

Phenology. Flowering May–July.

Distribution (Fig. 11). Throughout the Great Basin in northern Nevada and southeastern Oregon, east into the Snake River Plains of southern Idaho, west in California to the vicinity of Mt Shasta, and north in Oregon along the east side of the Cascades to Deschutes and Crook Counties; on basalt derived substrates in sagebrush desert or sagebrush-juniper communities; 1000–3000 m.

Scutellaria nana is readily distinguished from other taxa in the group by its dwarf habit, rhomboid to obovate leaves, white to creamy-yellow flowers, and red gynoecial disk. *Scutellaria sapphirina*, previously treated as a variant or variety of *S. nana* (Epling 1942; Cronquist et al. 1984), is distinguished from *S. nana* primarily by blue corollas that are shorter than those of *S. nana* and by a green-yellow gynoecial disk.

Scutellaria holmgreniorum Cronquist was described as a segregate of *S. nana*, differing from *S. nana* by the presence of prostrate stems, hairs on the stems that are spreading or upcurved, and gland-tipped hairs on the stems, leaves, and flowers (Cronquist 1981). Subsequent collections of this form from the type locality, and elsewhere in northeastern California and adjacent Nevada, exhibit erect stems

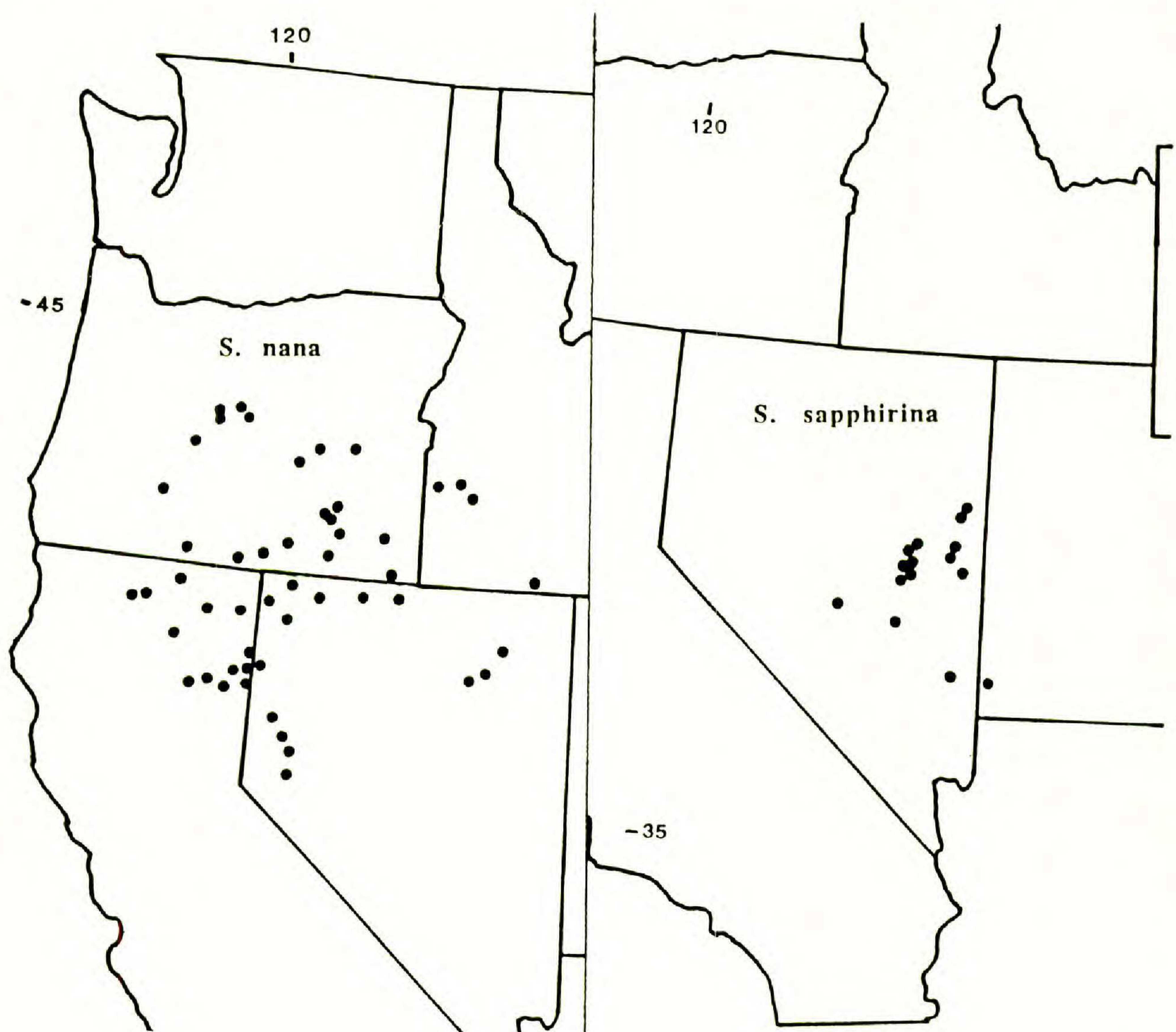


Fig. 11. Distribution of *Scutellaria nana* and *S. sapphirina*.

similar to *S. nana*. The presence of gland-tipped hairs is a character that is variable within most species of the *Scutellaria angustifolia* complex and is polymorphic within populations of *Scutellaria* near the type locality of *S. holmgreniorum* (Olmstead 581, 586; Schoolcraft 910B; Tiehm, Nachlinger & Schoolcraft 8809). Finally, although the gland-tipped hairs diverge from the stem nearly perpendicularly, in those plants with gland-tipped hairs, there are also shorter, eglandular hairs on the stem that are downcurved as in *S. nana*. Therefore, no specific, or subspecific, recognition seems warranted for *S. holmgreniorum*.

REPRESENTATIVE SPECIMENS: NEVADA. Elko Co.: Humboldt River, 10 mi SW Elko, *Holmgren* 967 (NY, UC); foothills of the Adobe range, E side of Suzie Cr, 3.2 mi ENE of Carlin, *Tiehm* 6067 (NY, RM); Mts N of Elko, *Ripley & Barneby* 5544 (CAS, NY). Humboldt Co.: Pine Forest Range, 2 mi N of Leonard Cr Ranch, *Holmgren & Reveal* 890 (MICH, NY, TEX, UC, WTU); Trout Cr Mts, Nine Mile Rd, 27 mi W of Orovada, *Holmgren & Holmgren* 9242 (NY, WTU); Sheldon Nat Wildlife Refuge, ridge S of Hell Cr, 5.6 mi SW of Virgin Valley ranch, *Tiehm & Rogers* 4421 (NY). Lyon Co.: summit on Hwy 95, 7.3 mi S of Fernley, *Olmstead* 588 (RENO, WTU); SE of Como, Pine Nut range, *Williams et al.* 82-306-1 (NY); 6.2 mi S of Fernley on Hwy 95, *Williams et al.* 80-55-1 (MO, NY). Washoe Co.: Mule Mt, 6.4 mi E of Sheldon National Wildlife Refuge sub-headquarters, *Tiehm & Rogers* 4308 (NY, WTU); 4.5 mi SE of Spanish Spring, *Saarni* 150 (RM, UC); 3 mi S of Vya, *Bacigalupi et al.* 5709 (JEPS); Granite range, Wall Canyon, 1.3 mi NE of last creek crossing, *Tiehm* 8104 (NY); Wadsworth, *M. E. Jones s.n.* (DS, GH, LA, MO, US); Pyramid Lake, *Kennedy* 1028 (DS, MO, NY, RM, UC, US); Buckhorn rd, 1.9 mi W of Buffalo Meadows rd on Buckhorn rd, T35N, R19E, *Tiehm et al.* 8808, 8809 (NY, WTU). Locale uncertain: "Nevada," *A. J. Jones s.n.* (MO).—CALIFORNIA. Lassen Co.: 1 mi S of rest area on Hwy 395, ca 16 mi S of Ravendale, *Olmstead* 415 (UC, US, WTU); 1 mi E of Westwood, *Heller* 15186 (MO, NY, UC, WTU); Pine Cr, *Baker & Nutting s.n.* (DS, RM, UC, US); along Smoke Cr NE of Viewland, *Ripley & Barneby* 5764 (CAS, NY); summit ridge SW of Diamond Mt, S of Susanville, *Stebbins & Jenkins* 2273 (GH, UC); ca 14 mi S of Ravendale and 13.2 mi E of Hwy 395 on Rye Patch Canyon rd, T33N, R16E, S36, *Olmstead* 584 (CAS, NY, WIS, WTU); N of Shinn ranch, T33N, R16E, S36, *Schoolcraft* 700 (NY); NW side of Shaffer Mt, 7.5 air mi NNW of Litchfield, T30N, R14E, S5, *Tiehm et al.* 8591 (NY, WTU); ca 14 mi S of Ravendale and 10.3 mi E of Hwy 395 on Rye Patch Canyon rd, T33N, R16E, S9, *Olmstead* 581 (UC, WTU); ca 14 mi S of Ravendale and 12.2 mi E of Hwy 395 on Rye Patch Canyon rd, T33N, R16E, S25, *Olmstead* 586 (UC, WTU); along rd to Big Spring, T33N, R16E, S11, *Schoolcraft* 910B (NY). Modoc Co.: top of mesa, 4.5 mi W of Alturas on Crowder Flat rd, *Holmgren & Holmgren* 8881 (NY); 5 mi S of Hackamore, *Howell* 12374 (CAS). Plumas Co.: 6 mi W of Chester, *Keck* 1720 (CAS, DS); near Lassen Buttes, *Brown* 613 (MO, NY, PH, US). Shasta Co.: Saddle Mt, W of Fall River Mills, *Stebbins & Jenkins* 2399 (DS, UC). Siskiyou Co.: road cut just S of Weed, *Baker* 13105 (UC); old logging above Hotlum Sta, N side of Mt Shasta, *Cooke* 30304 (NY, UC); W side of Shastina near the S bank of Diller Canyon, *Cooke* 15370 (CAS, LA, OSC); along old MacBride Springs rd, *Cooke* 16112 (GH, MO, PH); Igerna, *Heller* 8086 (DS, GH, MO, NY, PH, UC, US); Weed, *Smith* 390 (CAS, GH, US); Lava Beds Nat Monument, *Thompson* 13171 (MO, NY, WTU). Locale uncertain: "Great Basin," *Lemmon s.n.* (UC); "California," *Lemmon s.n.* (LA); E side of Sierras, *Congdon* 684 (GH); Sierra Nevada Mts, *Lemmon s.n.* (US).—OREGON. Crook Co.: head of Prineville Reservoir, 2 mi S of rd to Post, 16.8 mi SE of Prineville, *Olmstead* 693 (WTU); 17 mi SE of Prineville, *Cronquist* 7182 (DS, GH, MICH, MO, NY, RM, UC, WTU); Farewell Bend, *Leiberg* 472 (DS, GH, UC, US); Hay Creek, *Leiberg* 209 (NY, UC, US). Deschutes Co.: along rd to Lava Cast Forest, Paulina Mts, 3 mi E of Hwy 97, *Robbins & Eaton* 3610 (JEPS, RM); Tumalo, *Gilkey s.n.* (OSC, UC); 15 mi S of Bend, *Applegate* 4841, 4851 (DS, OSC); LaPine, *Peck* 9613 (GH, LA, MO, NY, OSC, PH); Bend, *Keck* 6747 (GH, OSC). Harney Co.: 13.3 mi S of Riley on Hwy 395, *Olmstead* 735 (WTU); Steens Mt, 7.3 mi from Frenchglen on rd to Fish Lake, *Olmstead* 726 (WTU); at end of gravel rd, 3.4 mi W of Fields, *Olmstead* 359 (OSC, WTU); 5 mi S of Princeton post office on rd to Diamond Craters, *Olmstead* 350 (OSC, WTU); low area between buttes, ca 8 mi N of Frenchglen, 2 mi E of Baca Lake, *Olmstead* 353 (WTU); 5 mi NW of Fields, *Maguire & Holmgren* 26408 (CAS, DS, GH, MO, NY, OSC, PH, RM, TEX, UC, US, WTU); 8 mi E of Frenchglen on rd to Fish Lake, *Maguire & Holmgren* 26436 (NY, UC, WTU); Stein's Mts, *Cusick* 1980 (GH, MO, UC, US); near Drewsy, *Leiberg* 2342 (GH, NY, UC); 4 mi E of Riley, *Holmgren & Tillett* 9611 (NY, UC); Alvord Cr, above ranch, E base of Steens Mts, 100 mi SE of Burns, *Cronquist* 8268 (GH, NY, TEX, WTU); Harney Valley, *Howell s.n.* (CAS, NY, OSC, PH, US, WTU). Klamath Co.: Crater Lake, *Coombs s.n.* (CAS); 2 mi SE of Klamath Falls, *Peck* 9448 (DS, GH, MO, NY, OSC, PH). Lake Co.: on bench above Drake Cr, ca 6 mi W of Adel on Hwy 140, *Olmstead* 362 (OSC, WTU); Hart Mt Nat.

Antelope Refuge, along S bdry rd, 1.6 mi S of jct with Camp Warner rd, 14.5 mi S of refuge headquarters, *Olmstead* 750, 751 (WTU); Goose Lake valley near Lakeview, *Peck* 15322 (DS, OSC); ca 10 mi S of Lakeview, *Eggleston* 7022 (NY, US). Malheur Co: 15 mi SW of Rome, *Peck* 21693 (OSC, UC); McDermitt Basin, *Packard & Grimes* 79-179 (NY). Locale uncertain: Williamson River, S Oregon, *Coombs s.n.* (CAS).—IDAHO. Ada Co.: 15 mi SE of Boise, *Christ & Ward* 7834 (NY); hill S of Tadpole Lake, Nat'l Guard Impact Area E of Swan Falls, *Ertter & Smithman* 4240 (NY). Owyhee Co.: Reynolds Cr Experimental Watershed, N of Dryden reservoir, *Bratz* B285-98 (NY). Twin Falls Co.: above Mule Cr crossing on Jackpot to Shoshone Basin rd, *Packard et al.* 79-132 (NY).

Scutellaria sapphirina (Barneby) Olmstead, comb. nov. *Scutellaria nana* var. *sapphirina* Barneby, Leaf. W. Bot. 5: 65. 1947.—TYPE: USA. Nevada: White Pine Co., White Pine Mtns, foothills W of Little Antelope, 6600 ft, 14 Jun 1944, *Ripley & Barneby* 6261 (holotype: CAS!; isotype: NY!).

Plants 5–10 (–20) cm tall, perennating by slender rhizomes swollen at the ends; stems branched near the base; stems and leaves moderately covered with trichomes 0.1–0.2 mm long and appressed-descending. Basal leaves with petioles 5–10 mm long; leaves below first flowering node short-petiolate to subsessile, the blades rhomboid to obovate, entire, the apices rounded; leaves above first flowering node subsessile, the blades rhomboid to oblong, the apices rounded; leaf at first flowering node 12–20 mm long, 4–7 mm wide, mean length/width = 2.8. Flowers axillary, first appearing 3–5 nodes above base of stem and continuing up the stem; pedicels 1.0–3.0 mm long; calyx 3.0–4.0 mm long, with concave transverse crest on upper lobe; corolla violet-blue, 13–17 mm long, personate, pubescent abaxially, pilose adaxially with long, tangled hairs, lower lip with white patch mottled with violet; filaments attached above the middle of the corolla tube; gynoecial disk green-yellow. Nutlets black, ovoid, 1.6–1.8 mm long, 1.2–1.4 mm wide, covered with small cylindrical to conical papillae, surrounded by a distinct circumferential band, sparsely covered with sessile glands. Chromosome number: $2n=24$. Figs. 4c,d, 10i–l.

Phenology. Flowering May–July.

Distribution (Fig. 11). Restricted to the White Pine mountains and a few adjacent mountain ranges in eastern Nevada and western Utah; open sandy or rocky soil, primarily of basalt origin, in sagebrush–juniper communities; 1500–3000 m.

Scutellaria sapphirina appears to combine characters of *S. nana* (habit, leaf morphology, and stem hair direction) and *S. angustifolia* subsp. *micrantha* (floral morphology). It lacks the derived characters of white corolla and red gynoecial disk of *S. nana*. The dwarf habit of *S. sapphirina* appears not to be a developmentally fixed character. In more mesic or shaded sites, it can develop an erect habit similar to *S. angustifolia*.

Epling (1942), recognizing the similarity in habit and pubescence, considered this taxon to be a variant of *S. nana* based on the observation of very few collections. Leonard (1927) considered specimens of this taxon to belong to *S. nevadensis* Eastwood (here placed in synonymy under *S. angustifolia* subsp. *micrantha*) on the basis of floral characters. However, it is quite distinct morphologically and one of the most distinct taxa in the group on the basis of isozyme analysis (Olmstead 1989).

REPRESENTATIVE SPECIMENS: NEVADA. Lincoln Co.: Clover Mts, 6.2 mi from Caliente on the Ella Mt rd, *Tiehm* 7971 (NY). Nye Co.: Quinn Canyon Range, on ridge E of Little Cherry Cr above the narrows, *Maguire & Holmgren* 25564 (GH, NY UC); 3.5 mi E of Currant, *Keck* 600 (DS, UC); White Pine Mts, Currant Cr Campground, 45 mi SW of Ely on Hwy 6, *Olmstead* 613 (WTU); Monitor Range, 0.5 mi NE of Hunts Canyon Guard Station, *Olmstead* 595 (RENO, WTU); Currant Cr, *Barneby* 14398a (NY); Monitor range, Hunts Canyon Guard Station, *Goodrich* 12058 (NY); 1.1 mi SW of Currant summit,

Williams et al. 79-103-1 (NY). White Pine Co.: N White Pine Ranges 0.8 mi N of Hwy 50, 0.6 mi E of Little Antelope summit, *Holmgren & Holmgren* 9350 (NY, RM, WTU); White Pine Mts, NE of Hamilton, *Ripley & Barneby* 9285 (CAS, NY); 4.2 mi S of Hwy 50 on eastern rd to Hamilton, *Raven & Solbrig* 13545 (GH, NY, UC); White Pine Mts, White River school district, 30 mi W of Ely, *Delameter s.n.* (DS); White Pine Mts, road summit between Currant Cr and White River drainages, *Holmgren et al.* 2165 (GH, MICH, NY, TEX, WTU); Becky Mt Homestead Cabin Canyon, 14 mi E of jct of Hwys 50 and 93, *Train* 3873 (NY, UC, WTU); White Pine Trail to White Pine Peak, *Ripley & Barneby* 9303 (NY); White Pine Mts, 0.8 mi NE of Currant Summit, ca 40 mi NE of Ely, *Olmstead* 614 (WTU); White Pine Mts, 7.9 mi N of Hwy 6 on Currant Cr rd at summit of road between White River and Currant Cr drainages, *Olmstead* 612 (WTU); White Pine Mts, 9.2 mi N of Hwy 6 on Currant Cr rd, *Olmstead* 611 (WTU); White Pine Mts, White River campground, 12.1 mi N of Hwy 6, via Currant Cr rd, *Olmstead* 609, 610 (OSC, RENO, UC, US, WIS, WTU); White Pine Mts, 1.8 mi N of White River campground on rd to Ellison Guard Station, *Olmstead* 607, 608 (WTU); White Pine Mts, 0.5 mi S of Jct Ellison Guard Station rd, *Olmstead* 606 (WTU); White Pine Mts, 2.9 mi S of Hwy 50 on Cottonwood Cr rd, *Olmstead* 600 (CAS, RENO, WTU); White Pine Mts, 1 mi N of Hwy 50 on rd 0.6 mi E of Little Antelope Summit, 38 mi E of Eureka, *Olmstead* 596 (NY, RENO, UC, WTU); Schell Cr range, East Cr canyon, 6.4 mi E of Hwy 93, 28 mi N of Ely, *Olmstead* 615 (WTU); Schell Cr range, 7.6 mi E of Hwy 93 on Schellbourne Pass rd, ca 45 mi N of Ely, *Olmstead* 617 (WTU); 7 mi E of Ely, *Hitchcock* 1286 (US); Six Mile Wash, 1 mi N of Lampson Canyon, *Thorne & Welsh* 1083 (NY); Hwy 6, 1.4 mi NE of Currant summit, *Williams* 80-71-1 (NY); near Illipah reservoir, *Williams & Tiehm* 80-237-3 (NY); Spring Valley rd, 11.2 mi S of Hwy 93, *Harrison & Thorne* 13172 (NY); across rd from Currant Campground, *Welsh* 20585 (NY).—UTAH. Washington Co.: 16 mi W of Enterprise, *Higgins* 14023 (NY).

Scutellaria siphocampyloides Vatke, Bot. Zeitung (Berlin) 30: 717. 1872.—TYPE: USA. California, *Bridges* 226 (holotype: B, destroyed; photo: UCLA!; lectotype, here designated: K!; isotypes BM! G! V!).

Scutellaria angustifolia var. *canescens* Gray in Brewer and Watson, Bot. Calif. 1: 603. 1880.—TYPE: USA. California: Santa Clara Co., Pacheco Pass, 20 Jun 1862, *Brewer* 1285 (lectotype, designated by Epling, 1942: GH!; isotypes: UC! US!).

Scutellaria austinae Eastwood, Bull. Torrey Bot. Club 30: 493. 1903. *Scutellaria angustifolia* var. *austinae* (Eastwood) Leonard, Contr. U.S. Natl. Herb. 22: 726. 1927.—TYPE: USA. California: Butte Co., Big Chico, May 1897, *Bruce* 1835 (holotype: CAS!; isotypes: NY! US!).

Scutellaria linearifolia Eastwood, Bull. Torrey Bot. Club 30: 493. 1903.—TYPE: USA. California: San Diego Co., San Diego, Jun 1876, *Fisher* 586 (holotype: CAS!; isotype: NY!).

Plants (10–) 20–40 (–55) cm tall, perennating by slender rhizomes swollen at the ends; stems single or branched near the base; stems and leaves moderately to densely covered with trichomes 0.1–0.2 mm long and appressed-ascending or rarely descending, often with gland-tipped trichomes, or occasionally glabrous. Basal leaves often turning red and then deciduous, with petioles 10–20 mm long; leaves below first flowering node short-petiolate to subsessile, the blades ovate, usually crenate, the apices rounded; leaves above first flowering node subsessile, the blades ovate to oblong, entire, the apices rounded; leaf at first flowering node (15–) 20–35 (–45) mm long, 4–8 mm wide, mean length/width = 5.7. Flowers axillary, first appearing 8–12 nodes above base of stem and continuing up the stem; pedicels 4.0–5.5 mm long; calyx 3.0–4.0 mm long, with concave transverse crest on upper lobe; corolla violet-blue, (23–) 25–30 (–35) mm long, personate, pubescent with gland-tipped trichomes abaxially, pilose with long hairs or glabrous adaxially, with scattered, long trichomes on the palate, the lower lip with white patch, with white patch mottled with violet spots, or uniformly violet-blue; filaments attached above the

middle of the corolla tube; gynoeceal disk green-yellow. Nutlets black, ovoid, 1.5–1.8 mm long, 1.3–1.5 mm wide, covered with small cylindrical papillae, surrounded by an indistinct circumferential band or none, sparsely to moderately covered with sessile glands. Chromosome number: $2n=24$. Figs. 1a,d, 3f–h, 10m–p.

Phenology. Flowering May–July.

Distribution (Fig. 12). The North Coast ranges of California from Siskiyou County to Napa County, the length of the Sierra Nevada foothills from Plumas County to Kern County, in the inner South Coast ranges from Alameda County to San Benito County, and in the mountains of southern California from Ventura County to San Diego County; moist openings and seeps and along dry streambeds in yellow pine woodland, digger pine woodland, oak woodland, and oak-shrub communities, occasionally on serpentine; 300–2300 m.

Scutellaria siphocampyloides is distinguished from *S. antirrhinoides*, with which it is sympatric in the North Coast Ranges of California, by a longer corolla, longer, narrower leaves, and gland-tipped trichomes on the corollas. *Scutellaria siphocampyloides* is morphologically most similar to *S. angustifolia* subsp. *angustifolia* and may be distinguished from the latter taxon by a more or less strongly reflexed lower corolla lip and a higher leaf length to width ratio. The two taxa are clearly distinguished on the basis of isozymes (Olmstead 1989) and geographic distribution.

Scutellaria siphocampyloides is a highly variable species found throughout the mountainous areas of California. Variation in leaf, flower, and pubescence charac-

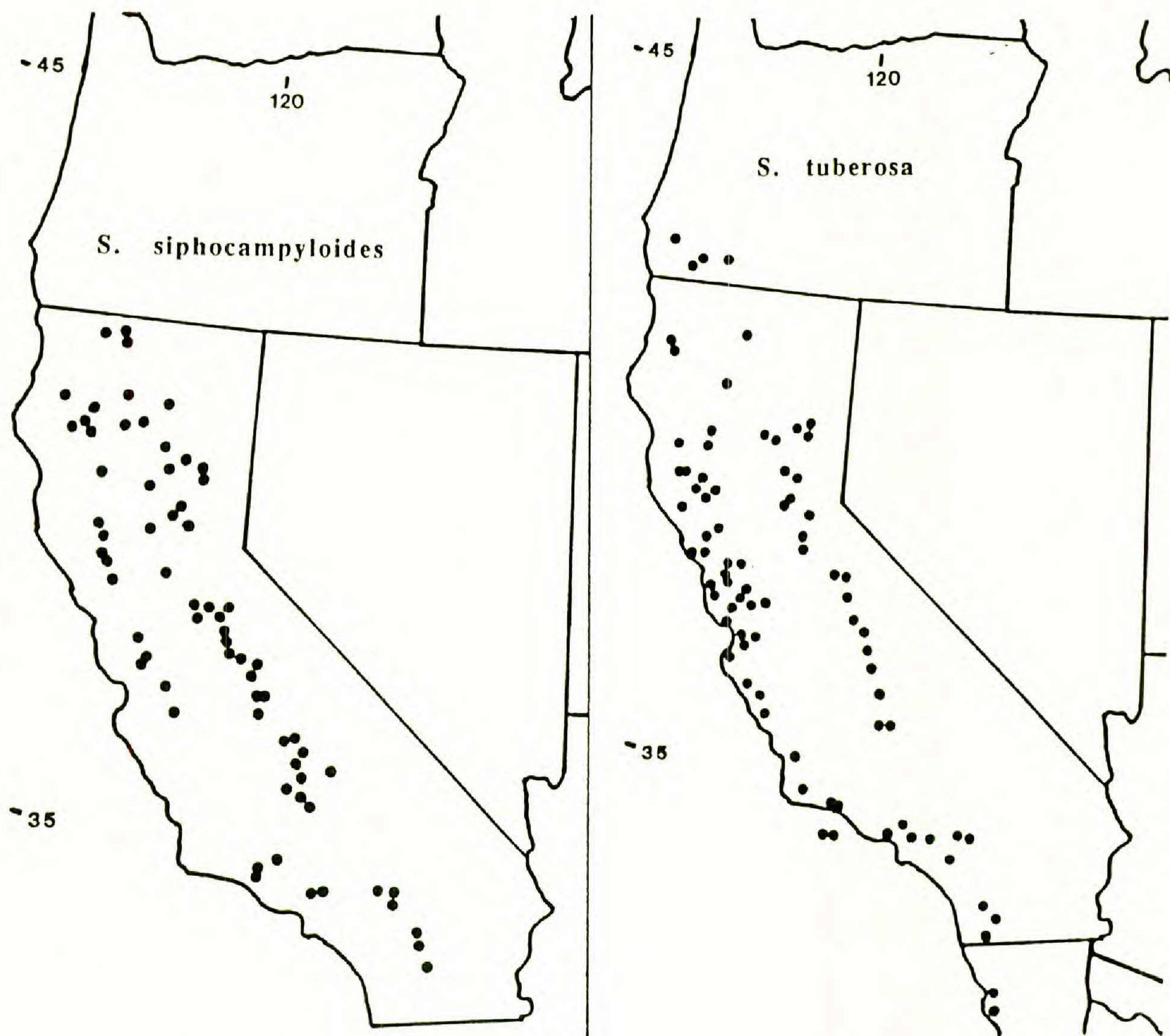


Fig. 12. Distribution of *Scutellaria siphocampyloides* and *S. tuberosa*.

ters resulted in the publication of four names in the early years of California botany. As more specimens were collected, the continuous nature of the variation in many characters led to a reduction in the number of recognized taxa culminating in the single species accepted here. In the most recent treatment of this group, Epling (1942) recognized *S. siphocampyloides* and *S. austiniae*, distinguished by the presence or absence of gland-tipped hairs on the stems, leaves, and flowers, and also characterized by differences in leaf shape (leaf l/w ratio of 5:1 for *S. siphocampyloides*, vs. 7:1 for *S. austiniae*). Examination of a large number of specimens in this study indicates that the leaf length-to-width ratio of these two forms does not differ significantly (5.75 ± 1.5 for *S. siphocampyloides* vs. 5.6 ± 1.5 for *S. austiniae*). The presence of gland-tipped hairs in this taxon, although restricted geographically to the central portion of the range, is a character that is polymorphic in almost every other species in the *S. angustifolia* complex and has been observed in at least one collection within this taxon to be polymorphic within a single population (Stebbins 6415). Experimental evidence from isozyme analysis indicates that there is no genetic differentiation between the forms characterized by the presence and absence of gland-tipped hairs and that populations of plants bearing the glands often are isozymically most similar to populations of eglandular plants and vice-versa (Olmstead 1989).

REPRESENTATIVE SPECIMENS: CALIFORNIA. Alameda Co.: Mocho Cr, *Elmer 4434* (MO, NY, UC, US); Hayward, *Soares s.n.* (JEPS); Arroyo Mocho, 16.5 mi from Livermore on Robert Livermore's place, *Lee & Carter 1541* (JEPS). Butte Co.: Butte Cr., in Butte Meadows campground, *Olmstead 418* (OSC, US, WIS, WTU); Chico Cr, E of Chico, *Heller 14397* (MICH, MO, NY, OSC, PH, RM, WTU, UC); Butte Cr, *Austin s.n.* (US); Chico, *Gray s.n.* (GH); Chico, *Bidwell s.n.* (GH); Butte Meadows, *Heller 12814* (GH, MO, NY, OSC, PH, US, WTU); Sutton House, head of Butte Cr, *Eggleston 7308* (NY, US). Calaveras Co.: 3 mi NW of Sheep Ranch on rd to San Andreas, *Olmstead 396, 398* (NY, OSC, WIS, WTU); Copperopolis, *Tracy 5605* (WTU, UC); near Milton, *Davy 1236* (UC); N Fork Calaveras River near San Andreas, *Jepson 9916* (JEPS); Mercer's Cave, *Hoover 2343* (JEPS, UC). Fresno Co.: Auberry rd, 0.8 mi W of Alder Springs, *Olmstead 568* (UC, WTU); Pine Ridge, *Hall & Chandler 242* (MO, NY, PH, UC, US); Tollhouse, *Hall & Chandler 39* (UC); Big Sandy Cr, *McDonald s.n.* (US); Trimmer Springs, Sierra foothills near Kings River, *Kelley s.n.* (JEPS). Humboldt Co.: Grouse Cr, *Chesnut & Drew s.n.* (UC). Inyo Co.: Owens Valley and at Ft Tejon, *Horn s.n.* (NY). Kern Co.: Telephone rd N of Rising Canyon, Tejon ranch, *Twisselman 11086* (CAS, OSC); Erskine Cr, Piute Mts, *Twisselman 8435* (CAS); Cedar Cr at Fulton Cr, *Farnsworth 143* (CAS); along Hwy 155, 2–3 mi W of Wofford Heights, *Olmstead 826, 828* (WTU); Weldon Meadow, Piute Mts, *Twisselman 7306* (CAS, TEX); near rd from Glennville to Pettit Ranch at Mill Cr crossing, *Smith 544* (JEPS, WTU). Lake Co.: 8.1 mi S of Middletown on Butts Canyon rd, ca 2 mi N of Napa Co. line, *Olmstead 367, 368, 574* (CAS, UC, US, WTU); Blue Oak campground, 35 mi E of Middletown on Hwy 20, 6.4 mi N on Walker Ridge, then 2.6 mi W on BLM rd to Indian Valley reservoir, *Olmstead 671* (WTU); Bartlett Springs rd, 0.8 mi W of Colusa Co. line at N end of Walker Ridge, *Olmstead 663, 665* (WTU); between Houghs Springs and the Colusa Co. line, *Heller 12386* (GH, NY, PH, UC, WIS); Complexion Canyon, E of Indian Valley, *Jepson 18963* (JEPS). Los Angeles Co.: Horse Flats campground, 3.0 mi N of Angeles Crest hwy on Horse Flats rd, *Olmstead 798* (WTU); Horse Flats rd, 2.0 mi N of Angeles Crest hwy, *Olmstead 794* (WTU); along creek, Chilao Camp, *Olmstead 792* (WTU); Liebre Mt, *McHargue & Miller s.n.* (OSC, WIS); Horse Flats, San Gabriel Mts, *Duran 3505* (GH, MO, NY, RM, WIS, UC, US); San Gabriel Mts, near Chilao Old Camp, *Thorne 39995* (MICH, UC). Madera Co.: NW edge of Bass Lake, *Constance 2350* (MICH, MO, NY, RM, WTU, UC); Bass Lake Ranger Station, N end of Bass Lake, *Olmstead 564* (WTU); along Hwy 41, 5.0 mi NE of Oakhurst, *Olmstead 562* (CAS, NY, WTU); NW shore of Bass Lake, 0.5 mi N of Forks Resort, *Olmstead 381* (CAS, NY, WTU). Mariposa Co.: Greeley Hill, above Coulterville, *Jepson 14931* (JEPS); Hell Hollow, 0.8 mi above Bagby on grade to Bear Valley, *Wolf 4852* (TEX, WTU, UC); along Hwy 49, ca 4 mi N of Mariposa on rd to Mt Bullion, *Ferris & Bacigalupi 10407* (GH, WTU); Mt Bullion, *Bolander 4946* (MO, NY, UC, US); Yosemite rd, 6 mi above Mariposa, *Fosberg 55032* (GH, NY); 1 mi SW of Pilot Peak, *Schlobohm 156* (RM, UC); *Hollick s.n.* (NY, US). Merced Co.: N slope of Twin Peaks, N fork of Los Banos Cr, inner South Coast ranges, *Mason 12280* (GH, MO, NY, WTU, UC). Napa Co.: Butts Canyon, *Jepson 18903* (JEPS); Napa-Soda Springs rd, *Sharsmith 5108* (UC). Nevada Co.: 2 mi E of Grass Valley, *Hall 275 & Essig 10178* (GH, MO, NY, RM,

WIS, UC); Nevada City, *Eastwood* 560 (GH, MO, NY, US). Plumas Co.: Prattville, *Platt s.n.* (JEPS); Indian Valley rd, *Sutcliffe s.n.* (CAS); Quincy, *Rose* 67156 (NY); Taylorsville, *Clemens s.n.* (NY); rocky hills, *Austin s.n.* (US); Ames *s.n.* (NY, PH, WIS). Riverside Co.: Keen Camp, San Jacinto Mts, *Munz* 5764 (UC); San Jacinto Mts, above James Reserve in Hall Canyon, *Thorne et al.* 38090 (DS); N Fork San Jacinto River, *Epling & Robison s.n.* (WTU); 1.1 mi SE of Mountain Center along Hwy 74, *Olmstead* 804 (WTU); Pine Cove, *Epling s.n.* (LA, MICH, MO, TEX, WTU); San Jacinto Mts, *Spencer* 1194 (GH, LA, NY). Sacramento Co.: Sacramento, *Baker & Nutting s.n.* (UC, RM). San Benito Co.: Clear Cr Canyon on jeep trail to Goat Mt, *Griffin* 4263 (JEPS); Hartman ranch, E side of Panoche Pass, *Hoffman* 1582 (UC). San Bernardino Co.: 2.1 mi N of Hwy 38 on rd to Seven Oaks, *Olmstead* 807 (WTU); San Bernardino Mts, upper Santa Ana, *Grinnell s.n.* (NY, US); San Bernardino, *Parish s.n.* (MO); Bear Lake, *Clokey* 5306 (GH, LA, NY, PH, RM, TEX, UC, US, WTU); Fredalba, San Bernardino Mts, *Abrams* 2778 (GH, MO, NY, PH, US, WTU); 2 mi above Converse Ranger Station, S fork Santa Ana River, *Kruckeberg* 3844 (WTU); San Bernardino Mts, *Parry & Lemmon* 337 (GH, MO, NY, PH); Bear Valley, San Bernardino Mts, *Parish* 3122 (MO, NY, US). San Diego Co.: Santa Rosa Mts, *Munz* 5854 (UC, RM); "San Diego Co.," *Gregory s.n.* (UC). Santa Clara Co.: San Antonio Cr, Burnt Hills, Mt Hamilton range, *Sharsmith* 3195 (UC); Santa Isabella Cr, E base of Mt Hamilton range, *Sharsmith* 1138 (UC); Gilroy, *Herrman s.n.* (NY); Coyote Cr, *Dudley* 4131 (GH, NY, US). Sierra Co.: "Sierra Co & etc.," *Lemmon s.n.* (GH, MO, NY, PH). Shasta Co.: 1 mi S of Boulder Cr, between La Moine and Dunsmuir, *Mason* 14752 (UC); Redding, *Blankenship s.n.* (JEPS); 25 mi E of Redding, *Hitchcock* 6500 (NY, UC, WTU); near Redding, *Heller* 7889 (GH, MO, NY, PH, US); Goose Valley, *Eastwood* 1015 (GH, MO, NY). Siskiyou Co.: along Klamath River, 1 mi W of jct of Hwys 96 and 99, N of Yreka, *Taylor* 4442 (UC); Yreka, *Heller s.n.* (NY), *Butler* 939 (UC); Horse Cr and Klamath River, *Rose* 45083 (GH, NY, WTU). Sutter Co.: Marysville Buttes, SE of N Butte rd to N Butte Foothills, *Lee* 2049 (JEPS); N Butte rd from E, *Ewan & Nester* 9560 (JEPS, LA, UC). Tehama Co.: Mineral, *Grinnell s.n.* (JEPS); Big Antelope Cr, 2 mi E of Andrews Station, *Jepson* 16624 (JEPS); 5 mi W of Paskenta, *Baker & Wagnon* 12693 (JEPS). Trinity Co.: 1 mi N of Junction City on Canyon Cr rd, *Olmstead* 677, 904 (WTU); Canyon Cr rd at Forty-dollar Gulch, 4 mi N of Junction City, *Olmstead* 456 (UC, US, WTU); Post Cr rd, 1–3 mi above jct with Hwy 36, ca 4–6 mi NE of Forest Glen, *Olmstead* 438, 439, 446 (CAS, NY, RENO, UC, WTU); Post Cr rd, 4 mi SW of Peanut, *Olmstead* 447 (NY, UC, WTU); Ditch Cr, Hwy 3, ca 2.5 mi S of Peanut, *Olmstead* 449 (WIS, WTU); forks of the Trinity River, *Rattan s.n.* (GH); Wildwood, *Bacigalupi et al.* 3387 (JEPS, UC); 1 mi N of Junction City, *Ferlatte & Rogers* 2033 (JEPS, WIS). Tulare Co.: Sequoia Nat Park, *Fry* 57 (JEPS); Middle Tule River, *Purpus* 5605 (GH, MO, UC, US); along the Middle Fork Kaweah River above Buckey Flat campground, 0.5 mi E of Hospital Rock, *Olmstead* 571 (WTU); Mineral King rd, 4.9 mi above Hammond, *Twisselman* 14246 (CAS); Slick Rock rd, W of Johnsondale, *Myrick* 1198 (CAS); Brush Cr, above confluence with N Fork Kern River, Hwy 190, 19.4 mi N of Kernville, *Olmstead* 831 (WTU); Kennedy Meadows, along banks of S Fork Kern River, *Olmstead* 813 (WTU); Kennedy Meadows, S Fork Kern River, *Griesel s.n.* (OSC); Lloyd Meadow, N side of Freeman Cr below jct with Lloyd Meadow Cr, *Smith* 1197 (JEPS, RM, WTU); Kern Lake region, *Culbertson* 4446 (GH, MO, NY, UC); Cedar Cr to Old Colony Mill, Sequoia Park, *Jepson* 653 (JEPS); 1 mi E of Hospital Rock, *Wagner* 257 (UC); Crystal Cave, Sequoia Park, *Hood* 45-120k (LA). Tuolumne Co.: Jamestown, *Jepson* 6310 (JEPS); along Wards Ferry rd, 2.5 mi NE of Groveland, *Olmstead* 388 (WTU); 1.5 mi S of Twain Harte Post Office, *Alexander & Kellogg* 3701 (GH, NY, RM, WTU, UC, US); Spring Gulch near Bear Cr, *Williamson* 24 (UC, US); Harden Ranch, Big Oak Flat-Yosemite rd, *Jepson* 10560 (JEPS); 1 mi SE of Taylor Hill, 1300 ft, *Belshaw* 2371 (UC); Hwy 108, 0.4 mi E of W exit to Twain Harte, *Wiggins* 21752 (DS, OSC). Ventura Co.: Sespe Cr, across from mouth of Potrero John Cr, 21 mi N of Ojai, on Hwy 33, *Olmstead* 782 (WTU); Sespe Cr area, along Hwy 33 at Tule Cr, 18.4 mi N of Ojai, *Olmstead* 785 (WTU); 1 mi above Chuchupate Ranger Station on rd to Frazier Mt, SW of peak, *Grant & Grant* 16039 (NY, WTU); Alamo Mt, *Hall* 6704 (UC); Sespe Cr at mouth of Cherry Cr canyon, *Pollard s.n.* (Tex); Frazier Mt, *Coville & Funston* 1197 (UC, US). Yuba Co.: 2 mi N of Oregon House, on rd to Forbestown, *Stebbins* 6415 (CAS); Brownsville, *Hill s.n.* (MO). Locale uncertain: Sierra Nevada, *LeConte s.n.* (PH); San Joachin Valley, *Meehan s.n.* (PH); Redstone, *Brandegge s.n.* (UC); Santa Rosa Mts, Ariz. (San Diego Co., CA?), *Epling & Simmons s.n.* (LA); Indian Valley, *Lemmon s.n.* (MICH, PH, UC); mountain canyons near desert, S California, *Spencer* 213 (LA); "California", *Fremont s.n.* (GH, MO, NY, US).

Scutellaria tuberosa Benth., Lab. gen. et sp. 441. 1834. *Scutellaria tuberosa* subsp. *australis* Epling, Madroño 5: 54. 1939, nom. superfl.—TYPE: USA. California: probably near Monterey, 1833, *Douglas s.n.* (holotype: K!).

Scutellaria pilosiuscula Nutt. ex Benth. in DC, Prodr. 12: 429. 1848, pro. syn.
Scutellaria tuberosa var. *similis* Jepson, Fl. W. Middle Calif. 454. 1901.
Scutellaria tuberosa subsp. *similis* (Jepson) Epling, Madroño 5: 54. 1939.—
TYPE: USA. California: Napa Co., new Pope Valley Grade near summit, 2
May 1893, *Jepson 14940* (holotype: JEPS!).

Plants 5–15 (–25) cm tall, perennating by tubers 0.5–2 cm long; stems single or branched near the base; stems and leaves moderately to densely covered with spreading multicellular trichomes 1.0–3.0 mm long. Basal leaves often turning red, with petioles 5–20 mm long; leaves below first flowering node short-petiolate, the blades ovate to cordate, crenate, the apices rounded; leaves above first flowering node short-petiolate to subsessile, the blades ovate, entire to crenate, the apices rounded; leaf at first flowering node (10–) 15–25 (–30) mm long, 5–10 (–12) mm wide, mean length/width = 2.1. Flowers axillary, first appearing 3–5 nodes above base of stem and continuing up the stem; pedicels 2.0–4.0 mm long; calyx 4.0–5.5 mm long, the upper lobe bearing a shallowly concave to subconical transverse crest; corolla violet-blue, 13–20 mm long, personate, pubescent with multicellular trichomes abaxially, pilose below the middle of the corolla tube with long, tangled hairs or glabrous adaxially, the palate densely covered with long trichomes or glabrous, the lower lip with central white patch mottled with violet; filaments attached above the middle of the corolla tube; gynoecial disk green-yellow. Nutlets black, turbinate, 1.5–2.0 mm in diameter, covered with large irregularly shaped papillae, with or without sessile glands, without a distinct circumferential band. Chromosome number: $2n=24$. Figs. 2a,b, 10q–t.

Phenology. Flowering April–May.

Distribution (Fig. 12). Coast Ranges from northern Baja California to southwestern Oregon and in the foothills of the Sierra Nevada from Kern County to Plumas County; commonly associated with chaparral vegetation where it is particularly evident in the first year following a fire, also found in oak (*Quercus kelloggii*) woodland communities; 200–1000 m.

Scutellaria tuberosa is morphologically, ecologically, and genetically the most distinctive species in the *Scutellaria angustifolia* complex (Olmstead 1989). It differs morphologically from other species in the group in having discrete tubers, rather than swollen, elongate rhizomes, a calyx crest that is only slightly concave to convex, and nutlet surface anatomy of roughly symmetrical polygonal cells rather than irregularly elongate cells. It differs ecologically from other members of the group in flowering phenology, a dormancy requirement for tuber sprouting, and preference for chaparral habitats. *Scutellaria tuberosa* also is distinguished readily by its crenate leaves and pubescence consisting of abundant long multicellular trichomes, characters it shares with *S. bolanderi*. These shared characters appear to represent a common ancestry for these two otherwise very different species.

The geographic and elevational distribution of *S. tuberosa* closely resembles that of other species of *Scutellaria* in California; however, it exhibits some unusual life history characteristics associated with its chaparral habitat. Under mature chaparral vegetation, *S. tuberosa* occurs as minute, unbranched plants, rarely greater than 5 cm tall, and rarely produces flowers at more than one node, or more than a single small tuber. In the first year following a fire, relatively large (10–25 cm), multibranched plants emerge that produce many flowers and tubers, dramatically increasing both the vegetative and seed reproduction output. In the second and third years following

a fire, *S. tuberosa* is inconspicuous or absent in the thick herbaceous vegetation that develops following a fire in chaparral communities (personal observation).

Two varieties, *S. tuberosa* var. *tuberosa* and var. *similis*, were recognized by Jepson (1901) based on difference in degree of pubescence on the calyx. He later commented that the distinctions between the varieties were of little significance (Jepson 1939). Epling (1939, 1942) accepted the distinction proposed by Jepson (1901) and redefined the two varieties as *S. tuberosa* subsp. *similis* based on Jepson's var. *similis* and *S. tuberosa* subsp. *australis* based on the type of the species (this latter taxon is correctly referred to subsp. *tuberosa*). Epling further characterized the subspecies by using characters of corolla pubescence. Epling's two subspecies represent a case of overlapping distributions of two apparently independent and variable characters: presence of hairs on the lower lip of the corolla, and presence of hairs within the corolla tube below the middle of the tube. The basis for subspecies recognition was the inverse correlation of these two characters in collections from the extreme northern and southern limits of the species distribution. These two characters are not strongly inversely correlated; there is a greater geographic distribution of intermediates, characterized by the presence of both or the absence of both pubescence states (Epling 1939), than of subspecies *tuberosa*. No subspecific taxa are here recognized.

REPRESENTATIVE SPECIMENS: U.S.A. CALIFORNIA. Alameda Co.: Berkeley Hills, *Newlon* 73 (JEPS); vicinity of Berkeley, *Walker* 40 (LA, UC); Arroyo Mocho, 10–30 mi S of Livermore, N end of Mt Hamilton range, *Sharsmith* 5406 (UC); Berkeley Hills, *Michener & Bioletti* s.n. (MO, NY, RM); Woolsey Canyon, Berkeley Hills, *Constance* 146 (PH); Oakland, *Holder* 2567 (UC, US); Strawberry Canyon, *Jepson* 14937 (JEPS, NY, US); Oakland, *Bolander* 6318 (GH, MO, NY, UC, US). Amador Co.: 6 mi N of Jones Butte, *Roseberry* 120 (UC); New York Falls, *Hansen* 118 (K, US). Butte Co.: canyon of Big Chico Cr, *Heller* 11231 (GH, NY, OSC, PH, UC, WTU); Little Chico, *Austin* 1836 (NY, US); Nelson Bar on Yankee Hill rd, W Fork Feather River, *Ingram & Ingram* 519 (WIS). Calaveras Co.: Mokelumne Hill, *Blaisdell* s.n. (GH, UC, US). Colusa Co.: College City, *King* s.n. (JEPS, UC). Contra Costa Co.: Moraga Ridge, *Epling & Stebbins* s.n. (LA); S of Camp 69, *Brewer* 1037 (UC, US); Marsh Cr, 4 mi E of Clayton, *Rose* 40250 (GH, MO); Mt Diablo, *Jepson* 14938 (JEPS). El Dorado Co.: Pacific House, *Brandegee* s.n. (UC). Fresno Co.: Bald Mt, 4.5 mi SE of Auberry, *Robbins & Heckard* 3564 (JEPS); Kings River canyon above Piedra, *Hoover* 3989 (UC). Glenn Co.: Long Point, N of Forest Hwy 7, 16 mi NW of Elk Creek, *Olmstead* 512, 515, 658 (CAS, WTU); along Forest Hwy 7, 10.4 mi W of Elk Creek-Paskenta rd, ca 14 mi NW of Elk Creek, *Olmstead* 660 (WTU). Humboldt Co.: along Seely-McIntosh rd, 1.5 mi from Willow Creek across the Trinity River, *Olmstead* 544 (CAS, WTU); 2 mi N of Willow Cr, *Anderson* 3644 (TEX); Trinity River Valley at Willow Creek, *Tracy* 16278 (UC, WTU); Hupa Valley, *Manning* 94 (UC). Kern Co.: hills between Lumreau Cr and Cedar Cr, *Farnsworth* 436 (CAS); Wildcat Cr, 2.3 mi ESE of Woody, *Smith* 341 (JEPS, WTU). Lake Co.: 5 mi W of Kelseyville along Highland Springs rd, *Olmstead* 535 (WTU); Walker Ridge, 2.4 mi N of Hwy 20 on Walker Ridge rd between Williams and Clear Lake, *Olmstead* 522, 524 (NY, OSC, RENO, UC, US, WIS, WTU); 1–3 mi up W side of Bartlett Grade, *Abrams* 12386 (NY); hills about Scotts Valley, 6 mi NW of Lakeport, *Tracy* 1686 (UC). Los Angeles Co.: Mandeville Canyon, Santa Monica Mts, *Clokey & Templeton* 4445 (GH, NY, UC, US); San Gabriel Mts, ridge top above Cobal Canyon, *Thorne & Henrickson* 32310 (WTU); Pasadena, *M. E. Jones* 3208 (MO, NY, UC, US); Hollywood, *Eastwood* 126 (PH); hills near Claremont, *Baker* 4756 (MO, NY, US); Santa Monica Forestry Station, *Barber* 46 (UC, MO). Madera Co.: San Joaquin Experiment Range, *Biswell* 178 (RM, UC). Marin Co.: Lucas Valley, N of Miller Cr rd, *de Nevers* s.n. (CAS); N slope of Big Rock Ridge, 2–3 mi W of Hamilton Field Air Base, *Robbins* 1511 (UC); between Bolinas and Fairfax, *Baker* s.n. (UC); Fairfax, *Michener & Bioletti* 5810 (MICH, US). Mariposa Co.: "Mariposa Co", *Hollick* s.n. (US); near Kinsley, *Hoak* s.n. (UC). Mendocino Co.: Willow Cr campground, Cow Mt Recreation Area, ca 5 mi E of Ukiah, *Olmstead* 536 (WTU); south Mill Cr, Ukiah, *Jepson* 9260 (JEPS); Longvale, *Tracy* 6221 (JEPS, UC); near Ukiah, *Bolander* 3929 (GH, MO, NY, UC, US). Monterrey Co.: Pacific Grove in pine woods, *Heller* 6649 (GH, MO, NY, PH, RM, UC, US); mouth of Strawberry Canyon, W of San Miguel Canyon rd, 3.5 mi N of Prunedale, *Tucker et al.* 3649 (OSC, WTU); Aromas, near Watsonville, *Meyer* 371 (UC); Santa Lucia Mts, *Plaskett* 60 (GH, NY, US); 8 mi N of Carmel Valley, Los Laurelos rd, *Rose* 57050 (NY); Hanging Valley, Santa Lucia Mts,

Breedlove 36239 (CAS). Napa Co.: Napa River basin, *Jepson s.n.* (MICH); Niebaum's Dam, SW of St. Helena, *Jepson* 14939 (JEPS). Nevada Co.: Moore's Flat, *Davis* 133 (NY, PH), Nevada City, *Eastwood* 519 (US). Placer Co.: Forest Hill, Newcastle, *Bolander* 4576 (NY, UC, US); near Auburn on rd to Grass Valley, *Eastwood & Howell* 4335 (UC). Plumas Co.: Rich Gulch, *Follett s.n.* (JEPS); hills E of Quincy, *Austin* 990 (US); Indian Valley, *Lemmon s.n.* (UC). Riverside Co.: Hagador Canyon, SW of Corona, *Glownke* 4626 (PH). San Bernardino Co.: one mi W of jct of Mill Cr and Yucaipa rds, *Finrock* 49 (UC); Rialto, vicinity of San Bernardino, *Parish s.n.* (MO, WTU); San Bernardino Mts, *Parry & Lemmon* 338 (GH, MO, NY, US). San Benito Co.: San Juan Canyon, *Pieters s.n.* (MICH). San Diego Co.: Smith's Mt at SE base, *Hall s.n.* (UC); Barrett, *Epling & Robison s.n.* (UC); Ramona, *Brandegee s.n.* (NY, PH, UC); Santa Ysabel, *Henshaw* 122 (US); Hwy 79, 8 mi S of Cuyamaca, *Holmgren & Jensen* 3572 (NY). San Luis Obispo Co.: Santa Lucia Mts, *Barber s.n.* (UC); Price Canyon, *Condit s.n.* (UC). San Mateo Co.: Crystal Springs Lake, *Baker* 447 (GH, K, MICH, MO, NY, RM, TEX, UC, US); Jasper Ridge, *McGregor s.n.* (MO); Stanford University, *Abrams* 2355 (MO); Belmont, open hills, *Rose* 35140 (MICH, WTU). Santa Barbara Co.: Santa Cruz Island, hills above Prisoner's Harbor, *Fosberg* 7692 (LA); Island of Santa Cruz, *Brandegee s.n.* (JEPS, UC); first canyon E of Prisoner's Harbor, Santa Cruz Is, *Fosberg* 7659 (MO, PH); near Pelican Bay, Santa Cruz Is, *Moran* 749 (MO, NY); Santa Barbara, *Brewer* 357 (US); Carpinteria, *Brewer* 266 (US); 0.8 mi NE of Refugio Pass, *Axelrod* 454 (RM); Santa Clara Co.: foothills W of Los Gatos, *Heller* 7288 (GH, MO, NY, OSC, PH, RM, UC, US, WIS); Smith Cr at foot of Mt Hamilton, *Heller* 8521 (GH, MO, NY, PH, US, WIS); Milpitas, *Smith s.n.* (PH). Santa Cruz Co.: Santa Cruz, *Reed s.n.* (US); 2.5 mi S of Grizzly Bear Cr, *Belshaw* 2325 (UC). Shasta Co.: Oak Station W of Redding, *Blankenship s.n.* (JEPS); 1 mi W of Redding city limit on Hwy 299, *Maze et al.* 774 (NY). Siskiyou Co.: near base of Mt Shasta, *LeConte s.n.* (PH). Sonoma Co.: W slope of Hood Mt, *Baker* 11695b (UC); Trinity Mt, E of Glen Ellen, *Howell* 12891 (LA, PH, UC); Pine Mt, near the Geysers, *Bolander* 3962 (US). Stanislaus Co.: near mouth of Arroyo del Puerto canyon, E side of Mt Hamilton range, *Sharsmith* 1765 (UC). Tehama Co.: 5 mi W of Paskenta, *Baker* 12557 (UC). Tulare Co.: Auckland Ranch, SW of Badger, *Mason* 11811 (RM, UC); N Fork Tule River, *Purpus* 5696 (UC). Tuolumne Co.: Big Oak Flat rd, 2.5 mi W of Smith Station (Burch Meadow), *Bacigalupi* 9244 (JEPS); Tioga rd, near Curls Inn, *Hutchison* 713 (UC); 2 mi ENE of Groveland, *Belshaw* 1923 (UC). Yuba Co.: vicinity of Dobbins, *Mason* 3728 (UC). Locale uncertain: "California," *Bridges* 313 (NY, US).—OREGON. Curry Co.: Rogue River canyon, Hellgate, *Peck* 24065 (OSC). Jackson Co.: 2 mi N of Central Point, *Peck* 14971 (OSC, WTU); near Wimer, *Hammond* 329 (NY, US). Josephine Co.: 1 mi S of Selma, *Gale* 27 (GH, PH, WTU); Grant's Pass, *Howell* 1252 (UC); near Grants Pass, *Sweetser s.n.* (LA, PH); Grants Pass, *Howell s.n.* (NY, PH, US, WTU); Grants Pass, *Piper s.n.* (UC, US).—MEXICO. BAJA CALIFORNIA. Las Trancas, *Kappler* D37-8-3-7 (LA); Santo Tomás, *Brandegee s.n.* (UC); 17 mi S of Enseñada, *Dressler* 471 (GH); Vallecito, *Orcutt* 1343 (GH, NY, PH, US).

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LITERATURE CITED

- Bentham, G. 1832. Bot. Reg. 18: pl. 1493.
 ———. 1834. *Labiatarum genera et species*, 419–445. London: Ridgeway and Sons.
 ———. 1848. Labiatae. In *Prodromus systematis naturalis regni vegetabilis*, vol. 12, ed. A. De Candolle. Paris: Treuttel & Würtz.
 Briquet, J. 1895. Labiatae. In *Die natürlichen Pflanzenfamilien*, eds. A. Engler and K. Prantl, IV (3a): 225–227. Leipzig: Wilhelm Engelmann.
 Cantino, P., and R. Sanders. 1986. Subfamilial classification of Labiatae. Syst. Bot. 11: 163–185.

- Collins, J. L. 1976. A revision of the annulate *Scutellaria* (Labiatae). Ph.D. Dissertation, Vanderbilt University, Nashville.
- Cronquist, A. 1981a. *An integrated system of classification of flowering plants*. New York: Columbia University Press.
- . 1981b. A new species of *Scutellaria* (Lamiaceae) from California. *Brittonia* 33: 449–450.
- Cronquist, A., A. Holmgren, N. Holmgren, J. Reveal, and P. Holmgren. 1984. *Intermountain flora*, vol. 4. Bronx, N.Y.: New York Botanical Garden.
- Epling, C. 1939. Notes on the Scutellariae of western North America. *Madroño* 5: 49–80.
- . 1942. The American species of *Scutellaria*. *Calif. Publ. Bot.* 20: 1–146.
- Erdtman, G. 1945. Pollen morphology and plant taxonomy. IV. Labiatae, Verbenaceae, and Avicenniaceae. *Svensk Bot. Tidskr.* 39: 279–285.
- Gill, L. S. 1981. Chromosomal evolution and incidence of polyploidy in the Canadian Labiatae. *Rev. Cytol. Biol. Veget.-Bot.* 4: 331–339.
- Gill, L. S., and J. K. Morton. 1978. *Scutellaria churchilliana*—hybrid or species? *Syst. Bot.* 3: 342–348.
- Gray, A. 1878. *Synoptical flora of North America*. New York: Ivison, Blakeman, Taylor Co.
- Hamilton, A. 1832. *Esquisse d'une monographie du genre Scutellaria*. Lyon: Louis Perrin.
- Heckard, L., and J. Hickman. 1985. The vascular plants of Snow Mountain, North Coast Ranges, California. *Wassman J. Biol.* 43: 1–42.
- Jepson, W. L. 1901. *The flora of western middle California*. Berkeley: Encina Publ. Co.
- . 1939. *Flora of California*, vol. 3. Berkeley: Associated Students Store, University of California.
- Kruckeberg, A. R. 1984. *California serpentine: flora, vegetation, geology, soils and management problems*. Berkeley: Univ. California Press.
- Lane, T. M. 1978. The Great Plains species of *Scutellaria* (Lamiaceae): a taxonomic revision. MS thesis, Kansas State Univ., Manhattan, Kansas.
- . 1983. Mericarp micromorphology of Great Plains *Scutellaria* (Labiatae). *Southwestern Naturalist* 28: 71–89.
- . 1986. *Scutellaria*. In *Flora of the Great Plains*, ed. T. M. Barkley. Lawrence: University Press of Kansas.
- Leonard, E. C. 1927. The North American species of *Scutellaria*. *Contrib. U.S. Natl. Herb.* 22: 703–748.
- Linnaeus, C. 1735. *Systema naturae*. Stockholm.
- . 1753. *Species plantarum*. Stockholm.
- Munz, P. 1959. *A California flora*. Berkeley: Univ. California Press.
- Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89: 583–590.
- Olmstead, R. G. 1988. Systematics, genetic diversity analysis, and phylogeny of the *Scutellaria angustifolia* complex (Labiatae). Ph.D. dissertation, University of Washington.
- . 1989. Phylogeny, phenotypic evolution, and biogeography of the *Scutellaria angustifolia* complex: inferences from morphological and molecular data. *Syst. Bot.* 14: 320–338.
- . In press. Biological and historical factors influencing genetic diversity in the *Scutellaria angustifolia* complex (Labiatae). *Evolution*.
- Penland, C. W. 1924. Notes on North American Scutellarias. *Rhodora* 26: 61–79.
- Porter, T. C. 1894. *Scutellaria brittonii*. *Bull. Torrey Bot. Club* 21: 177.
- Soltis, D. 1980. Karyotypic relationships among species of *Boykinia*, *Heuchera*, *Mitella*, *Sullivantia*, *Tiarella*, and *Tolmiea* (Saxifragaceae). *Syst. Bot.* 5: 17–29.
- Torrey, J. 1828. *Scutellaria resinosa*. *Ann. Lyceum Nat. Hist. New York* 2: 232.

APPENDIX

Chromosome numbers for *Scutellaria* and the allied genus *Salazaria* in North America. Voucher specimens for numbers first reported here are deposited at WTU.

SCUTELLARIA ANGUSTIFOLIA COMPLEX

- S. angustifolia* subsp. *angustifolia*: $2n=24$. Oregon: Wheeler Co., 16 mi N of Spray, *Olmstead* 640.
- S. angustifolia* subsp. *micrantha*: $2n=24$. Oregon: Harney Co., 3 mi E of Frenchglen, *Olmstead* 351.
Idaho: Elko Co., Owyhee R, 1 mi N of Wild Horse Dam, *Olmstead* 630.
- S. antirrhinoides*: $2n=24$. Oregon: Jackson Co., 2 mi W of Rogue River, *Olmstead* 656.
- S. bolanderi*: $2n=24$. California: Amador Co., Jackson, *Olmstead* 401; Fresno Co., 9 mi S of Tollhouse,

- Olmstead* 570; Calavaras Co., 2 mi W of Vallecitos, *Olmstead* 390; Calavaras Co., 1 mi N of Sheep Ranch, *Olmstead* 395.
- S. brittonii*: $2n=22$. Colorado: Boulder Co., 4 mi N of Ward, *Olmstead* 642.
- S. californica*: $2n=24$. California: Lake Co., Bartlett Springs, *Olmstead* 371; Lake Co., Blue Oak C.G., Indian Valley Reservoir, *Olmstead* 534; Mendocino Co., 8 mi E of Willits, *Olmstead* 542; Trinity Co., Canyon Creek at Ripstein Camp, *Olmstead* 540.
- S. nana*: $2n=24$. Oregon: Harney Co., 3.4 mi W of Fields, *Olmstead* 359. California: Lassen Co., 16 mi S of Ravendale, *Olmstead* 415; Lassen Co., Rye Patch Canyon Rd, ca 30 mi SE of Ravendale, *Olmstead* 581.
- S. sapphirina*: $2n=24$. Nevada: White Pine Co., Little Antelope Summit, 38 mi E of Eureka, *Olmstead* 596; White Pine Co., 0.8 mi E of Currant Summit, 40 mi SE of Ely, *Olmstead* 614.
- S. siphocampyloides*: $2n=24$. California: Calavaras Co., 3 mi NW of Sheep Ranch, *Olmstead* 396; Madera Co., N end of Bass Lake, *Olmstead* 564.
- S. tuberosa*: $2n=24$. California: Glenn Co., 16 mi NW of Elk Creek on FH 7, *Olmstead* 515; Mendocino Co., Willow Creek C.G., 5 mi E of Ukiah, *Olmstead* 536.

OTHER NORTH AMERICAN SPECIES OF SCUTELLARIA AND SALAZARIA

- Salazaria mexicana* Torr.: $2n=ca\ 50$ (Raven et al. 1965).
- Scutellaria alabamensis* Alexander in Small: $2n=30$ (Collins 1976).
- S. altamaha* Small: $2n=30$ (Collins 1976).
- S. arenicola* Small: $2n=30$ (Collins 1976).
- S. bushii*: $2n=30$ (Collins 1976).
- S. churchilliana* Fern.: $2n=60$ (Gill & Morton 1978).
- S. elliptica* Muhl.: $2n=30$ (Collins 1976).
- S. floridana* Chapman: $2n=30$ (Collins 1976).
- S. galericulata*: $2n=32$. Washington: King Co., Juanita Bay, Lake Washington, *Olmstead* 503; $n=16$, $2n=32$ (Gill & Morton 1978).
- S. glabriuscula* Fern.: $2n=30$ (Collins 1976).
- S. incana* Bieler: $2n=30$ (Collins 1976).
- S. intergrifolia* L.: $2n=30$ (Collins 1976).
- S. lateriflora* L.: $n=44$, $2n=88$ (Gill & Morton 1978).
- S. leonardi* Epling: $n=10$ (Gill 1981).
- S. mellichampii* Small: $2n=30$ (Collins 1976).
- S. montana* Chapman: $2n=30$ (Collins 1976).
- S. multiglandulosa* Small ex Harper: $2n=30$ (Collins 1976).
- S. parvula* Michx.: $n=10$ (Gill 1981).
- S. pseudoserrata* Epling: $2n=30$ (Collins 1976).
- S. serrata* Andr.: $2n=30$ (Collins 1976).